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CALIFORNIA'S HISTORIC LEGACY FOR LANDSCAPE CHANGE, THE WIESLANDER VEGETATION TYPE MAPS

JAMES H. THORNE[1] AND THUY N'GOC LE
Department of Environmental Science and Policy,
University of California, Davis, CA
[1]jhthorne@ucdavis.edu

ABSTRACT

This paper presents the digitized edition of the Wieslander Vegetation Type Maps (VTMs). The VTMs were part of the first statewide systematic survey of California's vegetation, conducted 1928–1939. Under the direction of Albert Wieslander, crews recorded the patterns of vegetation that they observed from vantage points across the state. The survey covers 176,901 km^2 including border and lake polygons and 165,652 km^2 of landscapes that we describe in more detail. There are 251,541 polygons in the full extent of the maps, with 249,630 in the analysis extent. These polygons are annotated with codes indicating the dominant plant species, for which voucher specimens were collected. The maps contain 655 species codes, representing 535 species or sub-species in 229 genera, including 34 *Arctostaphylos* Adans. and 16 *Quercus* L. species. The 249,630 polygons contain 26,013 unique combinations of species and levels of disturbance. These can be classified into 525 vegetation alliances or provisional alliances using the 2009 edition of the Manual of California Vegetation, or into 53 of the simpler California Wildlife Habitat Relationships (WHR) classes. The most extensive WHR types in the VTMs are Annual grasslands (25,733 km^2) Chamise-redshank chaparral (14,771 km^2), Mixed chaparral (9314 km^2), and Coastal Scrub (7088 km^2). California's Southwestern ecoregion is the most completely surveyed, with 93% of the area mapped, followed by the Central Western ecoregion (88.2%, including the Bay Area), the Sierra Nevada (71.6%), and the Great Valley (39.7%). The VTMs in these ecoregions provide a baseline for assessment of landcover change across large areas, and are an important legacy of the biogeographic patterns of plants and vegetation in California. This paper provides the methods used to digitize the collection and suggestions about how the data may be properly used in future studies.

Key Words: biogeography, ecology, historical landscape monitoring, VTMs, Wieslander Vegetation Type Maps.

The Wieslander Vegetation Type Map (VTM) Project was an effort to inventory the forests and natural lands of California. Lands were surveyed by United States Forest Service (USFS) crews under the direction of Albert Wieslander between 1928 and 1939. It has been considered among the finest vegetation maps ever made in the western hemisphere, and foundational for the subsequent development of other landcover mapping efforts such as the Soil Vegetation Survey (Küchler 1967). In addition to the vegetation maps, ~18,000 vegetation plots were surveyed, over 3000 photographs taken, and over 25,000 VTM voucher specimens were collected (Wieslander 1935a, 1935b, 1935c, 1986). Additional maps were produced showing the location of the plots and photographs. This remarkable vegetation survey eventually ended due to funding restrictions during World War Two. The entire collection of reference materials was housed at the University of California, Berkeley, where parts of it were nearly thrown away on two occasions, but survived and in the last decade photographs, maps, and original vegetation plot cards have been registered into the collections of the UC Bancroft Library (2008). The VTM herbarium voucher specimens are housed at the UC Berkeley Jepson Herbarium (JEPS). Systematic efforts to digitize the collection began around 2002 and have produced a database of the plot data with online access (http://vtm.berkeley.edu/), and also online access to scanned versions of the photographs (http://www.lib.berkeley.edu/BIOS/vtm/) (Kelly et al. 2005; Kelly et al. 2008). Digital production of the vegetation maps is the subject of this paper.

As anticipated by Wieslander (1935a), the Vegetation Type Map Project materials have formed the basis for many studies and publications, particularly the plot data, for which we provide a separate list of publications (Appendix 1). There are several references pointing to the intent to use plot and map data together for landscape assessments (Weeks et al. 1934, 1943; Wieslander and Jensen 1946; Wieslander 1986). The VTM vegetation maps were used in early assessments of regional conditions which include a general assessment for Eldorado County (Weeks et al. 1934) and a land use study across the entire northern Sierra Nevada, which includes a map of forest fire perimeters (Weeks et al. 1943). Elevational transect maps of California dominant trees and vegetation were developed (Critchfield 1971) and statewide maps of California's tree ranges (Griffin and Critchfield 1972) and shrubs (Sampson and Jespersen 1963) have been published. Regional studies that used the VTMs include a landcover change study (Bradbury 1974) and grassland dynamics (Freudenberger et al. 1987). Scans of the VTMs

were used as base data for the first edition of California's Gap Analysis Program vegetation maps (Davis et al. 1995, Davis et al. 1998). Efforts to digitize the VTMs (Kelly et al. 2005; Thorne et al. 2006) have resulted in the digital GIS versions of the VTMs becoming available. These have been used in a few local or regional landscape studies to date, including landscape change and conservation studies in the Bay Area (Thorne et al. 2013; Santos et al. 2014). The maps have also been used in studies on the dynamics of small Sierra Nevadan mammals (Santos et al. 2015), of forest change in the Sierra Nevada (Thorne et al. 2008) and for an educational movie about Sierra Nevada forest dynamics (Thorne and McQuinn 2012).

Albert Wieslander organized the field survey crews, many of whose names are found on VTM quadrangles throughout the duration of the survey. These crews were responsible for all the data collected, and they compiled each data type at the same time. The crews followed detailed protocols for all parts of the survey, which was established by 1933, and that are provided in the field manual (Wieslander et al. 1933, Wieslander et al. unpublished [1933] a, Wieslander et al. unpublished [1933] b). For the field creation of the vegetation maps, these include establishing view points on ridges, and tracing the patterns of the observed vegetation onto topographic maps. Up to nine dominant species were then recorded by species codes, written in the polygons where they were observed. At the start of this work, aerial photography was not yet developed, and was not used during this study, although in most instances the surveyors were looking down on, or laterally across a valley to, the vegetation they were mapping. Sixteen of the vegetation map quadrangles were published by the USFS, a beautiful series of maps with heavily annotated margins. Few collections of this series have survived. These published VTM quadrangles are of reduced detail relative to the original survey maps because of the limited space available in paper maps. The entire vegetation map collection has never been digitized.

The survey methods used to develop the vegetation maps were applied to large areas of the state, and were also used by the National Park Service (NPS), which produced maps for Lassen, Yosemite and Sequoia national parks, as an independent but coordinated effort to the USFS surveys. Areas outside the national parks were mapped by the USFS crews and were intended for use by natural resource managers, who would use the colors on the maps to identify different vegetation types for both timber and fire planning, and by researchers, who would use the more detailed species-specific information contained in each polygon for forestry, ecology, and landscape dynamics studies (Wieslander 1935a).

This paper presents the fully digitized VTM vegetation maps, a snapshot of California's vegetation in the 1930's. We describe the methods used to render the original maps to a geographic information system, report on the characteristics of the GIS product, and describe the extent and types of species and vegetation that were recorded. We identify the number of species reported, and the extent of landcover types according to the California Wildlife Habitat Relationship classification (WHR; Mayer & Laudenslayer 1988; California Department of Fish and Wildlife 2004), and the Manual of California Vegetation classification (MCV; Sawyer and Keeler Wolf 1995, Sawyer et al. 2009). We report the registration errors for each quadrangle, and provide a discussion of the types of analyses the maps have been used for, and their potential to inform future research and resource management.

METHODS

Scanning

The original VTMs were drawn on U.S. Geological Survey (USGS) topographic maps and in some cases U.S. Army Corps of Engineers maps, here termed base maps. Some of the base maps were originally surveyed as part of the coastal geodetic survey of the late 1800's (earliest topographic base maps surveyed in 1893). At the beginning of the VTM effort, only 30' quadrangles were available, and these make up the majority of the VTM extent surveyed. However, 15' quadrangles were used when those became available to the VTM crews, particularly in the San Francisco Bay Area and south along California' central coast. Additionally, some 7.5' quadrangles were used late in the survey effort. In all cases, when survey work on a quadrangle was completed, it was cut into sections, or 'tiles' (16 tiles for 30' quadrangles and four tiles for 15 and 7.5' tiles), and glued to a canvas backing to prevent loss of map data when the maps were folded (and they are stored folded). Reassembly of these maps was therefore the primary task of transitioning the patterns of species and vegetation to digital form. Most of these quadrangles were found in the collection at UC Berkeley. Thanks for recovery for some southern California quadrangle are due to the USFS office in Redlands; and to Michael Zinke, whose father, UC Berkeley professor Paul Zinke, helped survey some of the maps and who held some of them in his home; and to Sequoia, Yosemite and Lassen National Parks for allowing the maps in their collections to be scanned and added to the overall effort to digitize the collection.

We scanned the VTM vegetation map tiles individually, using a flatbed scanner at 300 dpi resolution. The tiles are arrayed four to each piece of canvas, meaning that the 30' quadrangles have four canvases per quad. The canvas was folded, and one or two tiles were scanned at each scan. The tiles are assigned a name according to the naming convention of the VTM maps: each quadrangle has a numeric code, and the tiles are numbered in counterclockwise rotational sequence with the upper right hand tiles

listed as A1, A2, A3, and A4; the upper left tiles as B1, B2, B3, and B4; the lower left quadrant tiles C1, C2, C3, and C4; and the lower right tiles as D1, D2 D3, and D4. This pattern is consistent across all tiles on all 30' maps. The four tiles comprising 15 and 7.5' quadrangle tiles are also numbered in counter-clockwise fashion, starting in the northeast corner. The 15' quadrangles codes are numeric followed by upper case letters (e.g., 105A, 105B, 105C, 105D), while 7.5' quadrangles are numeric followed by lower case letters (e.g., 88c, 88d, etc.). The scans are stored in a directory structure that reflects the schema used by the VTM project surveyors, of sequential numbers starting in the northeast corner of the state and running back and forth by each row of 30' quadrangle to the highest number, 192D for the quadrangle covering San Diego (Fig. 1).

The NPS effort covered Lassen, Yosemite and Sequoia National Parks. The Lassen and Sequoia National Park maps were created separately from the USFS VTMs. Protocols for VTM mapping in the national parks (Coffman 1934) mention that the effort was intended to support planning in different land cover types, in particular for fire hazard and protection planning, planning insect and disease control, determination of proper land use and treatment such as for "recreation, camp ground development, wild life, re-forestation, erosion control, etc.", augmenting knowledge concerning the flora and other natural features and providing an inventory as part of the nation-wide inventory survey. A report on the results of the VTM effort in Sequoia National Park (Frost 1935) identifies the effort as, "part of a vegetative-type survey of the State of California under the direction of the California Forest Experiment Station; and as a part of the nation-wide forest survey authorized by the McSweeney-McNary Research Act of 1928". There are two copies of the vegetation maps for Yosemite National Park; the NPS-surveyed copy that resides in that park shows only the area inside the boundaries of the park, while the USFS version is housed at the UC Berkeley Bancroft library and contains continuously mapped vegetation across the park boundary. It is difficult to determine which of these maps the original is; however we digitized the version from the UC Bancroft library, which has slight differences from the version in the Yosemite National Park archives.

Map Registration

The base topographic maps have been scanned by various map libraries around the state, particularly the University of California Berkeley Geology Library, University of California Santa Barbara Alexandria Digital Library, and California State University Chico Meriam Library California Historic Topographic Map Collection. These maps have typically been sheet scanned using a standard of 300 dots per inch (dpi) resolution, to produce an image file (.tif) of approximately 200 megabytes. We

obtained scans from these institutions, in many cases donated, to use in the digital development of the VTM quadrangles. We georeferenced the base maps using their corners and tic marks.

The base topographic maps use Clarke's spheroid of 1866 datum, and the polyconic projection, which was the standard for the U.S. Geological Survey during this time (U.S. Department of Commerce, Coast and Geodetic Survey 1917; Snyder 1983). The base maps were registered by projecting the degree-decimal geographic coordinates from the base map into a polyconic projection for the continental U.S., and using the central meridian for each individual base map. These polyconic coordinates were then used as control points to rectify the base map image. The registered base map was then used as the reference for registering each individual vegetation tile for that quadrangle.

Using ArcGIS (ESRI 2010), the scanned VTM tiles were registered onto the USGS topographic base maps, resulting in a projected version of the vegetation map, reassembled from the multiple tiles. We used 64 control points on the 16 digital VTM tile images, four per tile for a 30' quadrangle. Additionally, for 15' and 7.5' quadrangles, 16 control points were used on the four digital VTM tiles, four per tile. Control points were first selected based on matching geographic coordinates from the VTM tiles to the basemap. When geographic coordinates were not apparent (either faded or cut off), specific topographic lines with the border or parts of text that occur on both VTM tile and basemap were used. Once the digital topographic base map and VTM tiles were in their native projection, it was possible to digitize vegetation polygon boundaries, assemble polygons, and enter their vegetation attributes into the GIS.

Digitizing

Automated line digitizing options failed to efficiently record the complex patterns on the VTMs (Fig. 2). The hand-drawn and colored vegetation polygons on the original Wieslander VTM tiles were therefore digitized on-screen to create a digital polygon coverage of the Wieslander vegetation maps. On-screen digitizing was performed by hand-digitizing the polygon boundaries with a pen tablet using the registered VTM tile as the background image. A pen tablet (Wacom Digitizing Tablet; Wacom 2004) allows the user to draw polygon boundaries directly on the screen using a pen or stylus. Lines were digitized at an onscreen scale of no less than 1:6000 so that the precision of digitized lines was high, with <10 m spatial error introduced for line accuracy digitization (Thorne et al. 2006, 2008).

Attributing

Once the polygon layer had been created for a quadrangle, the species codes written on the maps
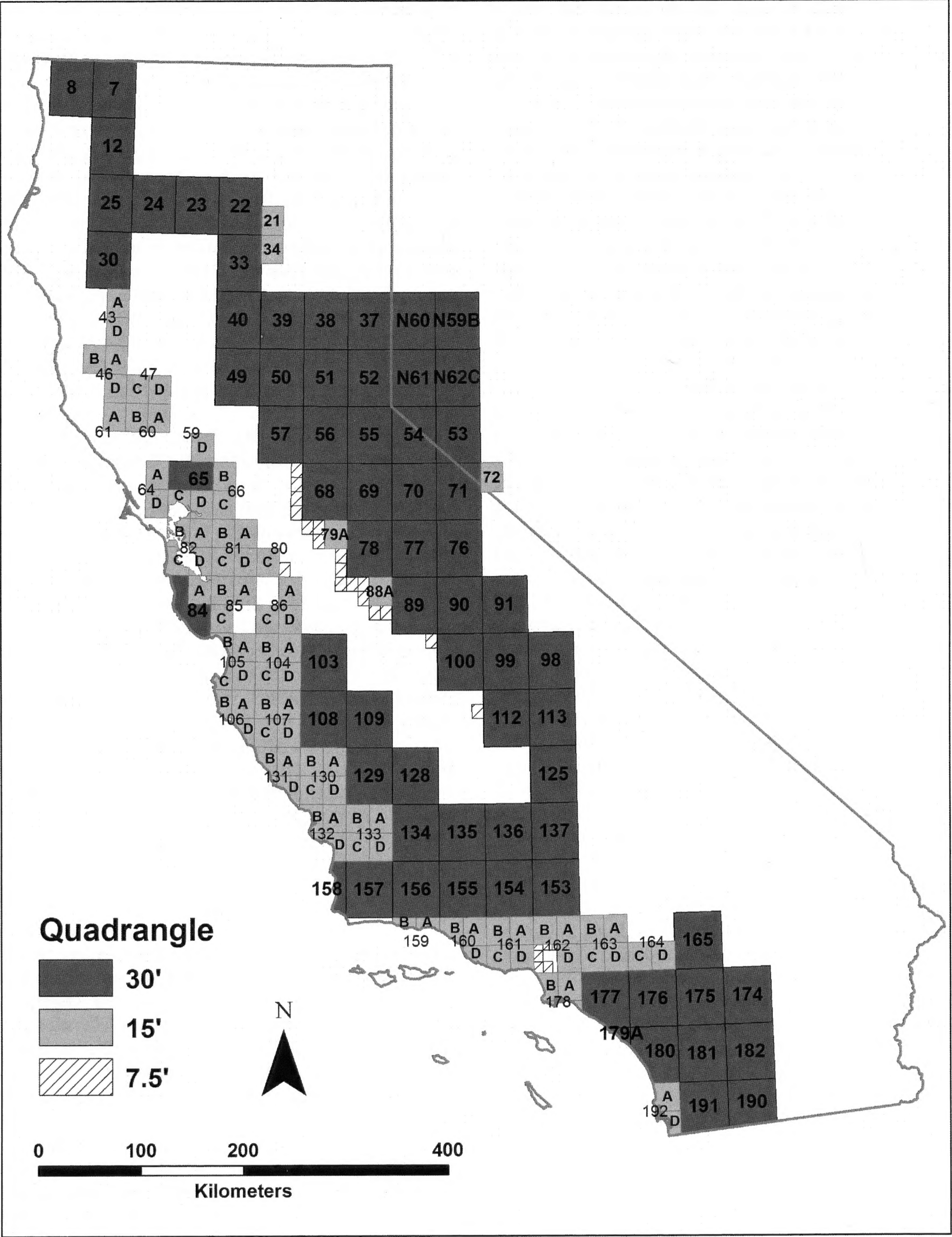
FIG. 1. The 30, 15, and 7.5 minute quadrangles surveyed during the VTM survey. The numbers are the VTM quadrangle ID numbers, while the letters represent the quarter quadrangles, which proceed counterclockwise from the northeast corner of any given quad. Quadrangle IDs are not shown for 7.5' quads.

were assigned to each polygon. There are multiple species codes for most polygons, reflecting the diversity of dominant trees, shrubs, and herbs in that polygon. Strings of species codes written in each

polygon consist of up to nine species codes. Single species records mean that species covered at least 80% of the polygon. Two or more species mean that no species covered at least 80% of a polygon. Species
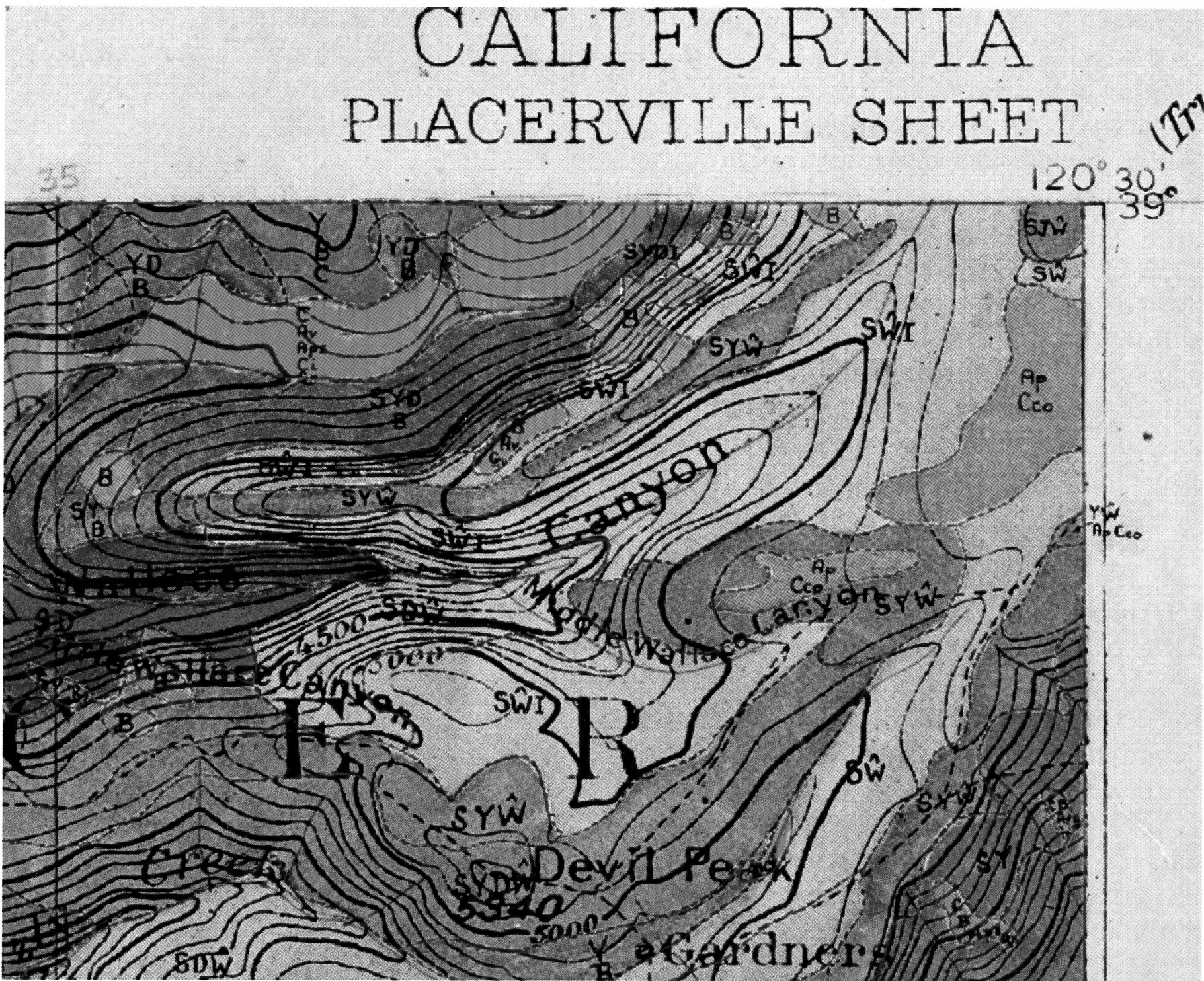
FIG. 2.   An example of part of a scanned VTM, quadrangle 56. Lines demarcating different types of vegetation were traced over at a resolution such that the digitized line (shown in red) is less wide than the VTM's polygon boundary. Lines demarcating different types of vegetation were traced over at a resolution such that the digitized line (shown in red) is less wide than the VTM boundary. The polygon colors refer to the vegetation types as the VTM crews defined them; the codes in the polygons refer to the dominant species recorded; and the vertical red lines refer to a recent burn. The complex topographic lines and text on the base map made automated generation of polygon boundaries impractical.

are presented in rank-order dominance, excepting mosaic polygons in which trees and then shrubs, or shrubs and then annuals/perennials are listed (Wieslander 1935a). The species codes were entered in the polygon attribute table in the same order as they appear in the polygon.

Since the attributing process required close inspection of each individual polygon to read the species codes recorded for it, this process also provided an opportunity to double check and correct the line digitizing work. The species codes on the maps were created by the Wieslander project, and are not standard taxonomic codes, and can be cryptic. A list of species and codes is available in the VTM field handbook. We digitized this list, and used it in addition to margin notes on various quadrangles, to develop a lookup table for translating codes to species names and to populate the GIS attribute table with plant species names. We used the first edition Jepson manual (Hickman 1993) as the standard nomenclature, but later provided the additional newly updated Jepson names (Baldwin et al. 2012) as determined through the Jepson Interchange website (http://ucjeps.berkeley.edu/interchange/). Most polygons consist of a single vegetation type.

However there are many cases where the species listed in polygons represent a mosaic of vegetation types within the polygon. Where these could be identified, species comprising the primary dominant type of the polygon were assigned two thirds of a polygon's area, and the secondary types one third (Thorne et al. 2008).

VTM polygons are also colored and in some cases marked with dashed lines that vary in their angle. The colors are the VTM assignment to major vegetation types, and the handbook identifies specific pencil brands and numbers to be used for specific vegetation types. The lines indicate that a polygon is in early seral condition at the time of mapping, due to either fire or logging. The cross hatching and angle was noted in the GIS attribute table. Explanation of the data fields is provided in Appendix 2.

From Species to Vegetation Types

The species strings from each polygon were used to assign vegetation classifications. We assigned vegetation and habitat types for the Manual of California Vegetation (MCV) classification system (Sawyer and Keeler Wolf 1995), and the California Wildlife Habitat relationships (WHR) Types (Mayer

and Laudenslayer 1988; California Department of Fish and Wildlife 2004). We used the colors in the original polygons to help confirm the vegetation type designation derived from our species- and seral condition-based vegetation designations. Polygons with mosaic types were given a primary and secondary MCV and WHR types. Some important and recurring species combinations were classified into provisional vegetation classes and habitat types if they had not yet been classified in the MCV. The second edition of the California MCV (Sawyer et al. 2009) was published during this phase of the work, and the final GIS attributes also provide a crosswalk to this classification.

Data Vetting

Species strings were checked when assigning MCV/WHR type names, and species found outside their known range were checked to make sure no transcription error had occurred when the codes were originally entered. Species strings were checked a second time in collaboration with a plant ecologist from the USFS, who used distribution and unusual combinations of species as a screen to seek for transcription errors. Major tree species extents were checked spatially with a tree species distribution publication (Griffin and Critchfield 1972), and other species were checked against the Jepson Interchange. Anomalies were corrected where possible, however some codes indicate "true" species occurrences beyond known extents or possible errors that we could not decipher. Accepted anomalies are notated in the comments field for the corresponding polygon in the final GIS products.

Evaluation of Registration Error

Historical map error was investigated using Root Mean Square Error (RMSE). The RMSE for each quadrangle was determined by georeferencing the VTM base map to a modern map. Modern reference maps used were Digital Raster Grids downloaded from the Cal-Atlas Geospatial Clearinghouse (http://portal.gis.ca.gov/geoportal). The RMSE in meters between the same locations on each VTM quadrangle and corresponding modern map was calculated by registering control points. These control points were selected from coordinate tick marks, mountain peaks, and some rail and road intersections, if evidence was the roads had not been moved. By choosing the same locations on both maps the spatial accuracy (RMSE) can be determined. The RMSE value indicates how far off any point can be on the base map by comparison to modern topography, and by extension the spatial error of the VTM map.

The RMSE value has been used as the basis for determining the size of grid cells to select to calculate changes on the landscape through comparison with contemporary landcover maps (Thorne et al. 2008). Since the RMSE indicates the spatial accuracy

between the historical and contemporary maps, selecting a grid cell size larger than a quadrangle's RMSE assures that the grid cells being compared through time overlap.

Map Compilation

We finalized two versions of each scanned VTM quadrangle, with and without the margins. The version with the margins cut off can be used to assemble visualizations of the original surveys for large extents of California. The margins in many cases contain considerable notes made by the surveyors, and were therefore retained in the second copy.

We generated the GIS version of the VTMs by quadrangle. Each quadrangle was completed as an original and is associated with the georectified scan of the topographic base map. The quad-by-quad VTMs were then combined, creating a single GIS of the entire survey. As each quadrangle was added to the compiled version, polygons that contained the same species combinations on either side of a quadrangle line were dissolved. In many cases, however, the adjacent species combinations differ, in which case the quadrangle line was retained. Finally, the data vetting exercises described above were conducted a second time on the final GIS layer.

This paper presents the summary information from the compiled digital work, including the number of species, extents of vegetation types, polygon size distribution, and RMSE values. We describe two versions of the GIS. The first includes large polygons on the edges of the survey that may be less well-mapped, and water bodies. The second, used for reporting extents of vegetation types, and information related to the vegetation such as the number of species, excludes the water bodies and large boundary polygons.

RESULTS

The VTMs digitized cover 70 30' quadrangles, 86 15' quadrangles, and 31 7.5' quadrangles (Figs. 1, 3). The extent mapped including the border and lake polygons is 176,901.5 km^2, and excluding them is 165,652 km^2 (Fig. 4), here called the "analysis extent" and used to report areas of landcover types. Of the total, 7541 km^2 including border polygons and 7299 km^2 excluding them occur in Nevada, near Reno, while the remainder are in California. Secondary WHR types in mosaic polygons occupy 2094 km^2 under both map extents.

The total number of polygons surveyed is 251,541 polygons in the full extent and 249,630 in the analysis extent. A good way to determine the resolution of the mapping is to examine the size distribution of the mapped polygons. The polygon size ranges from 0.34 ha to 137,195 ha for the full extent (Table 1) and to 86,933 ha for the analysis extent. The smallest polygon is a wetland also recorded on the USGS base map. For the full extent, the mean polygon size
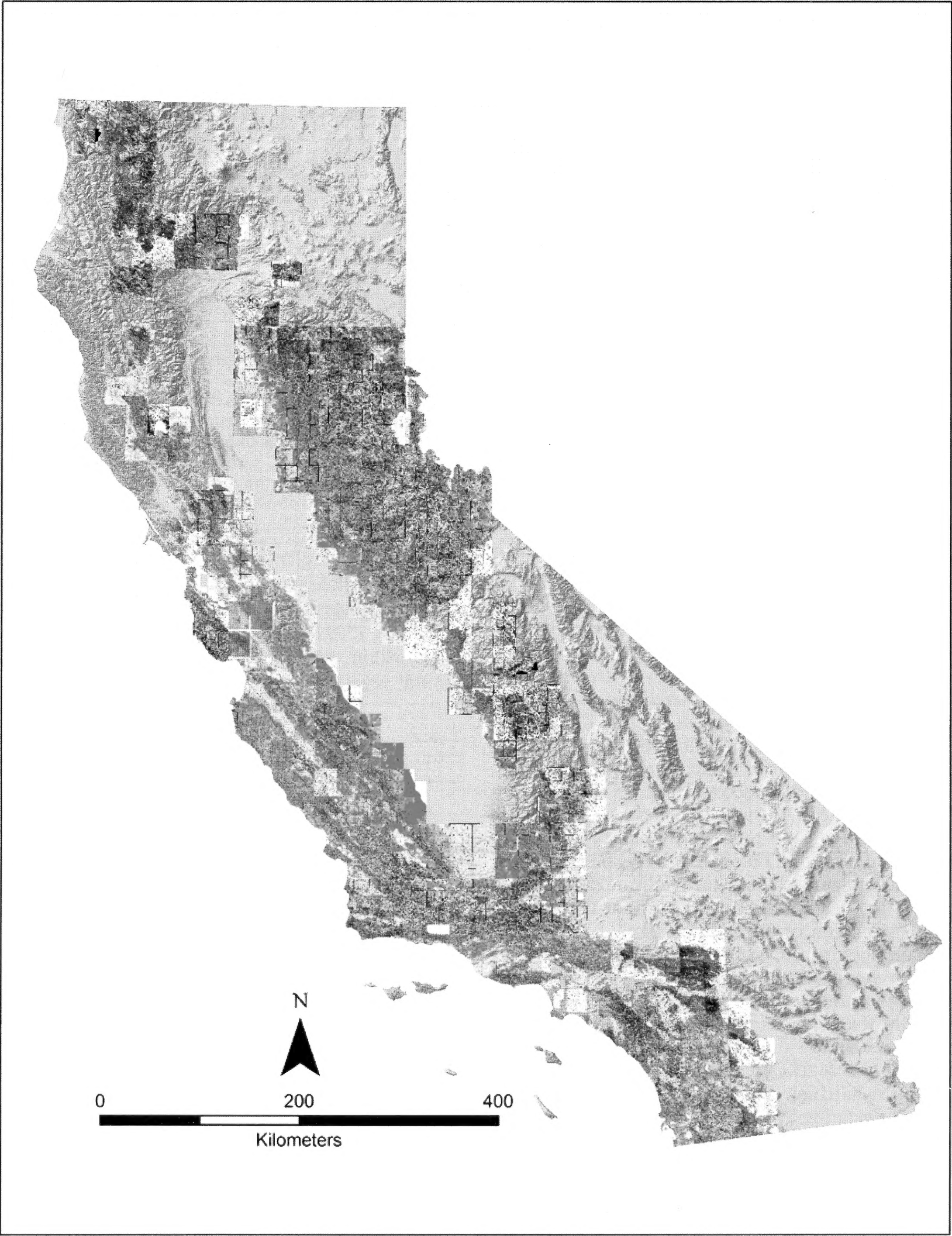
FIG. 3. Scans of the original VTMs showing the extent of the vegetation mapping.

is 70.3 ± 890.9 ha, while the median size is 12.9 ha. The maximum number of polygons is in the 8–16 ha size class, with 48,566. And, 54.5% of all the polygons range in size from 4–32 ha (Table 1).

The mean RMSE when registering the VTM topographic base maps to current topographic maps across all quadrangles is 59.7 m, median 48.3 m, and SD 50 m (Appendix 3). Seven quadrangles (five 30',
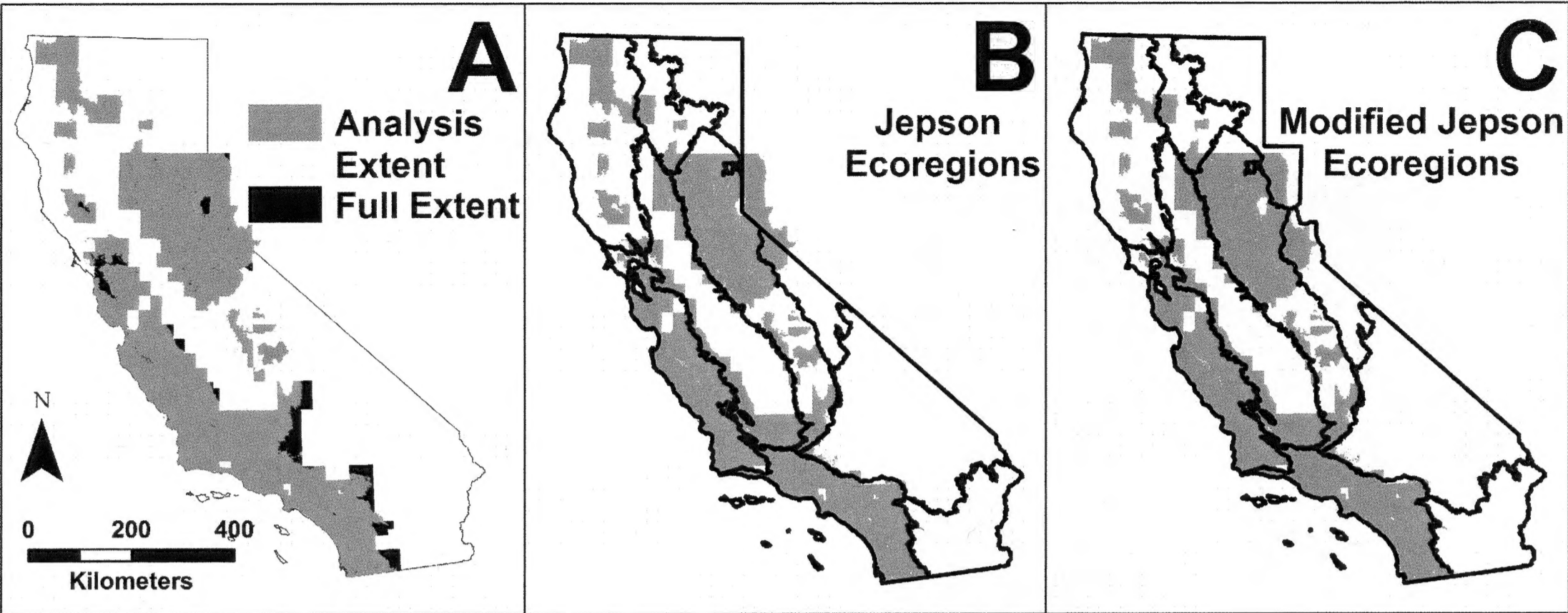
FIG. 4. Figure 4A portrays the extent of the VTM surveys with and excluding large water bodies and polygons on the borders of some surveyed areas. The map excluding border polygons is the one used for reporting extents of vegetation types, here called the "analysis extent". Figure 4B shows the extent of the analyzed maps overlaid on the Jepson (Hickman 1993) ecoregions. Because mapped areas extend beyond some ecoregion boundaries, we report ecoregional vegetation extents using modified ecoregions shown in Figure 4C. The two ecoregions we modified are the Modoc Plateau and East of the Sierra Nevada.

one full 15' and a partially surveyed 15') have RMSE above 150m.

There are 655 codes on the original maps (Appendix 4), representing 535 species or subspecies named in the maps. These represent 229 genera. There are 34 species or subspecies of *Arctostaphylos* Adans. identified, 12 for *Artemisia* L., 31 for *Ceanothus* L., 17 for *Eriogonum* Michx., 16 for *Pinus* L., and 16 for *Quercus* L. Thirty of the genus codes do not include a species name. There are eight codes for human-related landcover such as airport, residence, cultivated, etc., and 12 codes indicate habitat types ranging from rock and glacier, to deserts, marsh and meadow. There are 27 repeating codes but marked with parentheses which indicate the species is present but dead, snags after a burn, or that there is some cultivation or the area will likely be cultivated (specifically for the Cu code). There are 35 codes that refer to species that also have another code. There are seven unidentified codes, and we added a category for polygons with no species listed, termed 'no data'.

There are 26,013 unique combinations of species and cross-hatching codes. These were classed into 525 of vegetation Alliances or Provisional Alliances using the 2009 Manual of California Vegetation classifications (Sawyer et al. 2009), which correspond to 439 Alliances or Provisional Alliances in the 1995 version (Sawyer and Keeler Wolf 1995). The combinations also correspond to 53 California Wildlife Habitat Relationship Classes (Appendix 5; Mayer and Laudenslayer 1988; California Department of Fish and Wildlife 2004).We report historical landcover extents using the WHR classification, because of the lower number of landcover types into which the VTM species codes can be grouped. Those interested in the extents and patterns classed by

Alliance should refer to the GIS version of the maps. Across the whole survey, 98.7% of the landcover is in the primary class (163,547 km^2), and 1.2% is in the secondary (2094 km^2), indicating mixed vegetation types within those polygons (Table 2). Among the natural vegetation types, the lowest extents mapped

TABLE 1. The polygon size distribution of the mapped extent of the VTM survey.

Polygon size distribution by hectare size class	Number of polygons (full VTM survey extent)
0–0.25	147
0.5	468
1	2674
2	11,910
4	30,356
8	45,890
16	48,760
32	42,584
64	30,659
128	18,975
256	10,158
512	5016
1024	2242
2048	958
4096	379
8192	183
16,384	109
32,768	45
65,536	17
>65,536	11
Total # of polygons	251,541
Average size (ha)	70.33
Median size (ha)	12.95
Standard deviation	890.96
Polygon size range(ha)	0.034–137,195.80

TABLE 2. The mapped area of landcover types identified in the VTM survey, using California's Wildlife Habitat Relationships classification and the analysis extent of the VTMs (Fig. 4).

WHR	WHR name	Total WHR1 (km^2)	Total WHR2 (km^2)	Total (km^2)
ADS	Alpine Dwarf-Scrub	0.11	0	0.11
AGS	Annual Grassland	24,390	1343	25,733
ASC	Alkali Desert Scrub	1580	0	1580
ASP	Aspen	160	24	184
BAR	Barren	2360	1	2361
BBR	Bitterbrush	399	0	399
BCDF	Bigcone Douglas-Fir	406	15	421
BOP	Blue Oak-Foothill Pine	5628	0	5628
BOW	Blue Oak Woodland	5377	0	5377
COW	Coastal Oak Woodland	3941	0	3941
CPC	Closed-Cone Pine-Cypress	424	8	432
CRC	Chamise-Redshank Chaparral	14,763	8	14,771
CRP	Cropland	22,811	41	22,852
CSC	Coastal Scrub	7084	4	7088
DFR	Douglas Fir	4626	0	4626
DGR	Dryland Grain Crops	1	0	1
DRI	Desert Riparian	138	0	138
DSC	Desert Scrub	813	0	813
DSS	Desert Succulent Scrub	1	0	1
DSW	Desert Wash	152	0	152
EOR	Evergreen Orchard	0	0	0
EPN	Eastside Pine	553	0	553
EUC	Eucalyptus	83	0	83
FEW	Fresh Emergent Wetland	73	0	73
GLA	Glacier	1	0	1
JPN	Jeffrey Pine	4227	0	4227
JST	Joshua Tree	41	0	41
JUN	Juniper	1954	118	2072
KMC	Klamath Mixed Conifer	2466	0	2466
LAC	Lacustrine	5	0	5
LPN	Lodgepole Pine	1848	0	1848
LSG	Low Sage	130	0	130
MCH	Mixed Chaparral	9313	2	9314
MCP	Montane Chaparral	3707	2	3709
MHC	Montane Hardwood-Conifer	440	0	440
MHW	Montane Hardwood	6573	232	6805
MRI	Montane Riparian	242	49	290
PAS	Pasture	2	0	2
PGS	Perennial Grassland	715	0	715
PJN	Pinyon-Juniper	4278	0	4278
PPN	Ponderosa Pine	6604	0	6605
RDW	Redwood	715	12	727
RFR	Red Fir	3621	0	3621
SCN	Subalpine Conifer	1899	0	1899
SEW	Saline Emergent Wetland	605	0	605
SGB	Sagebrush	5631	0	5631
SMC	Sierran Mixed Conifer	6179	0	6179
UKW	Unknown	1684	0	1684
URB	Urban	1511	70	1581
VOW	Valley Oak Woodland	721	29	750
VRI	Valley Foothill Riparian	536	91	627
WFR	White Fir	1213	0	1213
WTM	Wet Meadow	926	46	972
	Total:	163,547	2094	165,641
	Overall Area			424,314.3
	Percent Area Mapped			39.0

include Alpine dwarf scrub (0.1 km^2), Desert Succulent Scrub (0.9 km^2), and Joshua Trees (41.01 km^2); while grasslands (25,733 km^2) Chamise-redshank chaparral (14,771 km^2), Mixed chaparral (9314 km^2), and Coastal Scrub (7088 km^2) are among the most extensively mapped natural vegetation types (Table 2). Agriculture covers and additional 22,852 km^2, there was 1581 km^2 of urban, 83

km^2 in Eucalyptus, and 1684 km^2 of unknown landcover, while only small amounts of the deserts were mapped (Fig. 4, Table 2).

Since the survey covers parts of 10 ecoregions, it is informative to examine landcover by ecoregion, which can provide a sense of the relative proportions of different landcover types within major ecoregions of the state (Table 3A–C). These tables provide the area of WHR landcover types using the analysis extent and the for modified Jepson ecoregions from the 1993 Jepson flora (Fig. 4C, Hickman 1993). The Southwestern ecoregion is the most completely surveyed region, with 93% of the area mapped, followed by the Central Western ecoregion (88.2%) which includes the Bay Area, the Sierra Nevada (71.6%), and the Great Valley (39.7%).

DISCUSSION

The Wieslander Vegetation Type Map project was the first attempted systematic survey of the forests and woodlands of California. Encompassing nearly half the state, it represents a tremendous opportunity for assessment of landscape change. The ecoregions with particular promise, because of the extent of surveys within them are the Central Western Coast, Southwestern Coast, the Transverse Ranges, and the Central and Northern Sierra Nevada Mountains. Large areas in the Klamath Mountains and west of Reno, NV were also mapped and could be used for landscape change analyses.

Most of the USFS administrative units in California had been established shortly before the survey, and three were established during the survey. The VTM maps and plot data were used by the USFS to make projections of timber volume and of land condition. Timber volume calculations in tabular form, derived from a 1930's combination of the VTM plot data and maps remain a part of the VTM collection that has not been analyzed, although the data are now digital. Assessments of timber could easily have become the focus of the VTM field effort, and critiques of the VTM plot data are that it is therefore biased in the direction of recording more forested areas and of biasing locations sampled towards relatively bigger trees than surrounding conditions (Bouldin 1999, Keeley 2004). However, the leader of the project, Albert Wieslander, asserts the actual methods used during his 1986 interviews for the Berkeley History project. He reminds us of what the VTM field manual instructs — that the surveyors were to map the existing vegetation, and that each vegetation plot surveyed concurrently with the mapping effort is intended to portray the average condition of the trees and shrubs of the polygon within which it was taken. Regarding the suggested bias towards big trees, both resurveys of VTM plots and comparisons of VTM plot data to contemporary independent plot data, have found declines in large trees (e.g., Lutz et al. 2009; Fellows and Goulden

2008; Dolanc et al. 2013; 2014; McIntyre et al. 2015). However, other historical comparison studies that do not use the VTM plot data (e.g., van Mantgem et al. 2007) have found similar patterns, so it seems difficult to prove that there is a bias in the VTM plot data. There is no way we know of to disprove the suggestions of over-estimation of tree size and oversampling of forest plots relative to forest proportion on the landscape, other than to point out that the head of the program had a different perception of how the data were to be recorded and used, that many of the VTM plot data locations are in chaparral, and that far more research publications have found utility in the VTM plot data (Appendix 1) than have determined it inaccurate (Bouldin 1999, Keeley 2004).

These critiques however, do not relate to the VTM's vegetation maps, which are the subject of this paper. Without doubt these make up one of the most complete and taxonomically extensive field survey efforts ever conducted in California (Colwell 1977). The results include one of the foundational collections of vascular plants for the Jepson Herbarium, which was used to confirm the species mapped, and cartographically exquisite (Figs. 5–9), highly information dense maps that portray large extents of the natural landscapes of California.

Approaches to Handling the Spatial Accuracy

We reproduced the VTM maps to their original level of spatial accuracy, and each map has varying levels of topographic fidelity relative to modern terrain maps. Our reasoning was that it was important to get an exact replica of the original VTMs. More intensive transformations of the VTMs to match modern topography are technically feasible, and have been conducted for two areas. Based on more than 14,000 total photo interpreted tiepoints in the Yosemite National Park VTMs (6793 total polygons), Walker (2000) recorded an RMSE in the park VTMs of 242.5 m. The latter could involve a convolution of 1980's-era digitizing errors, plus the original VTM errors. Positional errors were much more pronounced in some areas due to the compounding effects of extreme relief (which caused larger than average base map inaccuracies), and the difficulty of VTM crews in accessing adequate viewing vantage points, which even then often offered only high-oblique angles to look at the ground, such as across canyons. However, Walker's study did not have the benefit of scans of the original maps- he worked with polygons that another, unknown contractor had developed from the hardcopy maps, set upon a digitizing table. We observed similar patterns of higher RMSE in topographically complex regions, but generally found lower RMSE values for the majority of VTM quads after using the scans of the original maps for registration purposes.

In 2008, National Park Service vegetation ecologists at the Santa Monica Mountains National

TABLE 3A. The extent of WHR types mapped by the VTM survey within modified Jepson Ecoregions using the analysis extent (Fig. 4C). All area values are in km².

WHR	Cascade Ranges Total WHR1	Total WHR2	Total	Central Western CA Total WHR1	Total WHR2	Total	East of Sierra Nevada Total WHR1	Total WHR2	Total	Great Valley Total WHR1	Total WHR2	Total
ADS	0	0	0	0	0	0	0	0	0	0	0	0
AGS	163	79	242	6904	455	7359	16	3	19	11,511	266	11,777
ASC	0	0	0	3	0	3	1	0	1	1556	0	1556
ASP	1	0	1	0	0	0	77	5	82	0	0	0
BAR	44	0	44	160	0	160	220	0	220	41	0	41
BBR	4	0	4	0	0	0	17	0	17	11	0	11
BCDF	0	0	0	27	1	27	0	0	0	0	0	0
BOP	558	0	558	2088	0	2088	0	0	0	40	0	40
BOW	143	0	143	1822	0	1822	0	0	0	250	0	250
COW	0	0	0	2660	0	2660	0	0	0	4	0	4
CPC	6	0	6	116	1	117	0	0	0	0	0	0
CRC	0	0	0	4507	1	4508	0	0	0	6	0	6
CRP	78	0	78	6040	20	6059	54	15	69	7714	1	7715
CSC	0	0	0	2470	0	2470	0	0	0	148	0	148
DFR	38	0	38	65	0	65	0	0	0	2	0	2
DGR	0	0	0	0	0	0	0	0	0	0	0	0
DRI	0	0	0	0	0	0	0	0	0	131	0	131
DSC	0	0	0	5	0	5	185	0	185	177	0	177
DSS	0	0	0	0	0	0	0	0	0	0	0	0
DSW	0	0	0	2	0	2	0	0	0	110	0	110
EOR	0	0	0	0	0	0	0	0	0	0	0	0
EPN	0	0	0	0	0	0	50	0	50	0	0	0
EUC	0	0	0	53	0	53	0	0	0	1	0	1
FEW	0	0	0	28	0	28	0	0	0	1	0	1
GLA	0	0	0	0	0	0	1	0	1	0	0	0
JPN	132	0	132	13	0	13	56	0	56	0	0	0
JST	0	0	0	0	0	0	0	0	0	0	0	0
JUN	0	0	0	209	65	274	28	0	28	19	5	24
KMC	381	0	381	0	0	0	0	0	0	0	0	0
LAC	0	0	0	5	0	5	0	0	0	0	0	0
LPN	64	0	64	0	0	0	104	0	104	0	0	0
LSG	0	0	0	0	0	0	23	0	23	0	0	0
MCH	691	0	691	2233	0	2233	0	0	0	77	0	77
MCP	196	0	196	0	0	0	115	0	115	0	0	0
MHC	3	0	3	118	0	118	0	0	0	0	0	0
MHW	418	1	419	837	108	945	1	0	1	61	13	74
MRI	4	2	6	26	0	27	13	8	21	46	1	46
PAS	0	0	0	2	0	2	0	0	0	0	0	0
PGS	3	0	3	562	0	562	0	0	0	107	0	107
PJN	0	0	0	10	0	10	1185	0	1185	17	0	17
PPN	312	0	312	36	0	36	0	0	0	0	0	0
RDW	0	0	0	604	2	606	0	0	0	0	0	0
RFR	182	0	182	0	0	0	1	0	1	0	0	0
SCN	64	0	64	0	0	0	196	0	196	0	0	0
SEW	0	0	0	202	0	202	2	0	2	365	0	365
SGB	0	0	0	5	0	5	1840	0	1840	2	0	2
SMC	660	0	660	13	0	13	0	0	0	0	0	0
UKW	22	0	22	252	0	252	21	0	21	135	0	135
URB	1	0	1	464	4	468	1	0	1	43	0	43
VOW	16	0	17	442	11	454	0	0	0	63	7	70
VRI	1	1	2	192	14	207	0	0	0	142	13	155
WFR	20	0	20	0	0	0	5	0	5	0	0	0
WTM	8	1	9	36	0	36	158	5	164	195	0	195
Total:	4213	84	4298	33,212	682	33,894	4371	36	4407	22,978	304	23,282
Area of Ecoregion			20,754.8			38,412.6			18,925.4			58,630.3
Percent of Ecoregion Mapped			20.7			88.2			23.3			39.7

TABLE 3B. The extent of WHR types mapped by the VTM survey within modified Jepson Ecoregions using the analysis extent (Fig. 4C). All area values are in km^2.

WHR	Modoc Plateau and Nevada			Mojave Desert			Northwestern CA		
	Total WHR1	Total WHR2	Total	Total WHR1	Total WHR2	Total	Total WHR1	Total WHR2	Total
ADS	0	0	0	0	0	0	0	0	0
AGS	230	47	277	348	9	357	523	12	534
ASC	2	0	2	2	0	2	0	0	0
ASP	5	0	5	0	0	0	0	0	0
BAR	8	0	8	181	0	181	97	0	97
BBR	91	0	91	85	0	85	0	0	0
BCDF	0	0	0	0	0	0	0	0	0
BOP	0	0	0	7	0	7	272	0	272
BOW	0	0	0	6	0	6	304	0	304
COW	0	0	0	0	0	0	203	0	203
CPC	0	0	0	0	0	0	259	6	265
CRC	0	0	0	23	0	23	975	1	976
CRP	277	2	279	277	0	277	428	0	429
CSC	0	0	0	12	0	12	14	0	14
DFR	0	0	0	0	0	0	4218	0	4218
DGR	0	0	0	0	0	0	0	0	0
DRI	0	0	0	0	0	0	0	0	0
DSC	169	0	169	52	0	52	0	0	0
DSS	0	0	0	0	0	0	0	0	0
DSW	0	0	0	0	0	0	0	0	0
EOR	0	0	0	0	0	0	0	0	0
EPN	8	0	8	0	0	0	0	0	0
EUC	0	0	0	0	0	0	0	0	0
FEW	0	0	0	1	0	1	0	0	0
GLA	0	0	0	0	0	0	0	0	0
JPN	60	0	60	0	0	0	122	0	122
JST	0	0	0	37	0	37	0	0	0
JUN	751	0	751	334	2	335	0	0	0
KMC	0	0	0	0	0	0	2085	0	2085
LAC	0	0	0	0	0	0	0	0	0
LPN	4	0	4	0	0	0	18	0	18
LSG	26	0	26	0	0	0	0	0	0
MCH	0	0	0	150	0	150	674	0	674
MCP	51	0	51	0	0	0	798	0	798
MHC	0	0	0	0	0	0	124	0	124
MHW	0	0	0	2	0	2	1601	19	1620
MRI	4	1	5	1	0	1	12	1	13
PAS	0	0	0	0	0	0	0	0	0
PGS	0	0	0	1	0	1	25	0	25
PJN	523	0	523	139	0	139	0	0	0
PPN	2	0	2	0	0	0	584	0	584
RDW	0	0	0	0	0	0	111	10	121
RFR	2	0	2	0	0	0	776	0	776
SCN	5	0	5	0	0	0	20	0	20
SEW	11	0	11	0	0	0	0	0	0
SGB	2039	0	2039	14	0	14	0	0	0
SMC	0	0	0	0	0	0	0	0	0
UKW	41	0	41	6	0	6	771	0	771
URB	16	0	16	1	0	1	9	0	9
VOW	0	0	0	4	0	4	44	2	46
VRI	4	0	4	0	0	0	7	2	8
WFR	1	0	1	0	0	0	357	0	357
WTM	36	0	36	0	0	0	11	0	11
Total:	4364	51	4415	1683	11	1694	15,443	54	15,497
Area of Ecoregion			30,294.9			73,982.8			55,937.5
Percent of Ecoregion Mapped			14.6			2.3			27.7

TABLE 3C. The extent of WHR types mapped by the VTM survey within modified Jepson Ecoregions using the analysis extent (Fig. 4C). All area values are in km^2.

WHR	Sierra Nevada			Sonoran Desert			Southwestern CA		
	Total WHR1	Total WHR2	Total	Total WHR1	Total WHR2	Total	Total WHR1	Total WHR2	Total
ADS	0	0	0	0	0	0	0	0	0
AGS	2447	372	2819	5	0	5	2244	101	2345
ASC	3	0	3	0	0	0	13	0	13
ASP	77	19	96	0	0	0	0	0	0
BAR	1442	0	1443	4	0	4	164	0	164
BBR	166	0	166	0	0	0	26	0	26
BCDF	0	0	0	0	0	0	379	14	393
BOP	2653	0	2653	0	0	0	10	0	10
BOW	2843	0	2843	0	0	0	9	0	9
COW	0	0	0	0	0	0	1074	0	1074
CPC	26	0	26	0	0	0	18	0	18
CRC	920	5	925	31	0	31	8302	0	8302
CRP	884	2	885	1	0	1	7059	2	7061
CSC	21	0	21	60	0	60	4358	4	4362
DFR	303	0	303	0	0	0	0	0	0
DGR	1	0	1	0	0	0	0	0	0
DRI	0	0	0	0	0	0	6	0	6
DSC	32	0	32	13	0	13	180	0	180
DSS	1	0	1	0	0	0	0	0	0
DSW	0	0	0	0	0	0	40	0	40
EOR	0	0	0	0	0	0	0	0	0
EPN	495	0	495	0	0	0	0	0	0
EUC	0	0	0	0	0	0	28	0	28
FEW	0	0	0	0	0	0	42	0	42
GLA	0	0	0	0	0	0	0	0	0
JPN	3540	0	3540	0	0	0	303	0	303
JST	3	0	3	0	0	0	1	0	1
JUN	247	5	252	35	1	37	332	39	371
KMC	0	0	0	0	0	0	0	0	0
LAC	0	0	0	0	0	0	0	0	0
LPN	1591	0	1591	0	0	0	67	0	67
LSG	82	0	82	0	0	0	0	0	0
MCH	1797	2	1798	145	0	145	3545	0	3545
MCP	2489	2	2491	0	0	0	58	0	58
MHC	23	0	23	0	0	0	172	0	172
MHW	3042	92	3134	0	0	0	609	0	609
MRI	84	37	120	1	0	1	50	0	50
PAS	0	0	0	0	0	0	0	0	0
PGS	4	0	4	0	0	0	13	0	13
PJN	1305	0	1305	116	0	116	983	0	983
PPN	5016	0	5016	0	0	0	654	0	654
RDW	0	0	0	0	0	0	0	0	0
RFR	2660	0	2660	0	0	0	0	0	0
SCN	1614	0	1614	0	0	0	0	0	0
SEW	13	0	13	0	0	0	12	0	12
SGB	1444	0	1444	0	0	0	286	0	286
SMC	5254	0	5254	0	0	0	252	0	252
UKW	336	0	336	8	0	8	91	0	91
URB	29	0	30	0	0	0	946	65	1011
VOW	106	9	115	0	0	0	44	0	44
VRI	33	11	44	1	0	1	156	49	205
WFR	787	0	787	0	0	0	42	0	42
WTM	426	39	464	0	0	0	55	1	55
Total:	44,240	594	44,834	421	2	422	32,622	277	32,899
Area of Ecoregion			62,582.6			29,422.6			35,370.7
Percent of Ecoregion Mapped			71.6			1.4			93.0

FIG. 5.   Details of the original VTMs from the Oakland area and from the National Park Service Mapping in Lassen National Park.

Recreation Area hired Aerial Information Systems (AIS) to convert the original VTM hardcopy maps into an ArcMap geodatabase. They registered the maps and captured data one small area at a time, edge-mapping and redrafting the original vegetation polygons with reference to modern USGS basemaps and 2001 orthophoto imagery. All attribute data was captured, and all taxonomic references were updated with reference to the 1993 Jepson Manual. The NPS has used these digital maps in a number of projects to study vegetation dynamics. (R. Taylor, personal communication).

For broad landscape analyses, incorporating the spatial inaccuracies of the historic maps can be adequately addressed using a grid-based analysis in which the vegetation polygons are resampled to grids for change analysis by comparison to contemporary vegetation maps. To this end we provide the RMSE values of registering each quadrangle to modern topography (Appendix 3). This has proven effective for change analyses on a single 30' quadrangle in the Sierra Nevada (Thorne et al. 2008) and for a study in the Bay Area (Thorne et al. 2013). The RMSE errors suggest that analyses across large regions could be conducted at 100 m or 150 m resolution. Analyses for smaller areas and finer scales may need to consider further topographically-based modification of the VTMs. Such attempts should also consider the minimum mapping unit limitations of the VTMs. Generally, contemporary vegetation maps have finer spatial grain, and less taxonomic detail than the VTMs. The normalization of these map components with the contemporary data to be used is suggested for spatially-based landscape change analyses using the VTMs.

At the beginning of the survey, the VTM mapping used first edition USGS topographical quadrangles, which were part of the US Geodetic Survey and recorded topography onto 30' quadrangles, often from the late 1800's. The topographic base maps were nearly all developed prior to adoption of the North American Datum of 1927 (NAD27), meaning that the VTMs were drawn on topographic maps made using the 1866 Clarks ellipsoid datum and the polyconic projection (Gannet 1904, United States Department of Commerce, Coast and Geodetic Survey 1917, Beaman 1928, Snyder 1982). During the course of the survey, maps with greater spatial resolution became available and some of the later edition VTM quadrangles are presented on 15' and even 7.5' quads, and use the NAD27 datum. In all cases we converted the final GIS to NAD83, California Teale Albers projection. However, in cases where both 7.5' or 15' quadrangles exist as well as a 30' map, it appears that the finer-resolution quadrangles are copies from the original surveys, conducted using the 30' quadrangle.

Opportunities

An interesting perspective that archival agency data permit, is the tracking of prevailing practice and thought within agencies through administrative changes over time. Historians working for the NPS or the USFS infrequently describe this type of dynamic. However, it can be very valuable for the purposes of tracking landscape-scale dynamics to do so, because understanding how one program influenced the next can help with the integration of large survey datasets for analysis. In the case of the VTMs, the methods used were subsequently incorporated into the state of California's Soil Vegetation Survey mapping efforts. The Soil Vegetation Survey (SVS) was a collaborative program by the state, the USFS, and the University of California, which mapped much of California's natural lands and is spatially complimentary to the VTMS (Keeler-Wolf 2007). The SVS maps contain polygon-specific information about the soil types and species codes denoting dominant species in rank descending order for each polygon, which are the same as the codes used in the VTM maps. There was considerable overlap of personnel during the SVS program, including Wieslander himself, who was instrumental in developing and running the SVS program (Wieslander 1986). An important product that integrates the VTM maps with the SVS is the atlas of range maps for California's tree species (Griffin and Critchfield 1972). The digitization of the SVS is an opportunity to establish additional California reference conditions for vegetation, from the 1940's and 1950's, particularly for the northwest ecoregion, and potentially parts of the Sierra Nevada. Further investigation into how California's SVS and the National Resources Conservation Service's soil survey program (http://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/) correspond to each other; and into the relationship between the VTM's species-specific mapping efforts and later ones using the US National Vegetation Classification System (http://usnvc.org/) or other national landcover classifications, could allow an examination of the VTM results from broader spatial and mapping perspectives, and also might permit use of the detail in the VTMs to assess the quality of the national products.

The VTM maps contain more taxonomic information than available in modern landcover maps in California. Modern vegetation mapping efforts in California fall into two general classes; efforts that are specific to California and efforts that are part of more extensive mapping endeavors. There exist currently several California-specific vegetation mapping efforts including: the Manual of California Vegetation (MCV), the State government's most intensive and detailed mapping effort; a USFS product termed 'CalVeg' (http://www.fs.fed.us/r5/rsl/projects/mapping/accuracy.shtml); and the 'FRAP' map, a rasterized state-level effort to integrate the most current, detailed, and accurate maps available. It is produced by the California Department of Forestry and Fire Protection (http://frap.fire.ca.gov/). Each of these products provides more detail than any of the national-scale map
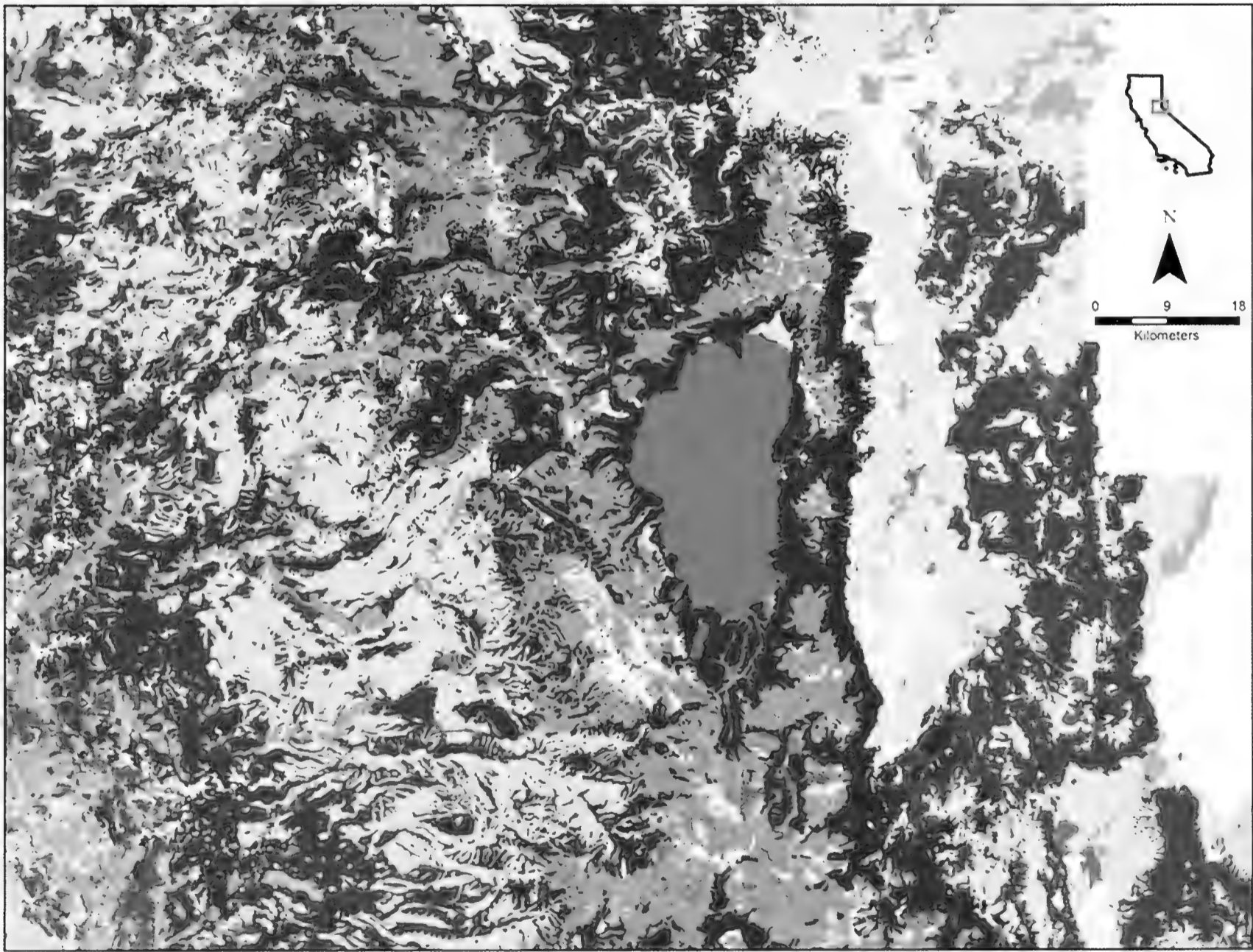
A
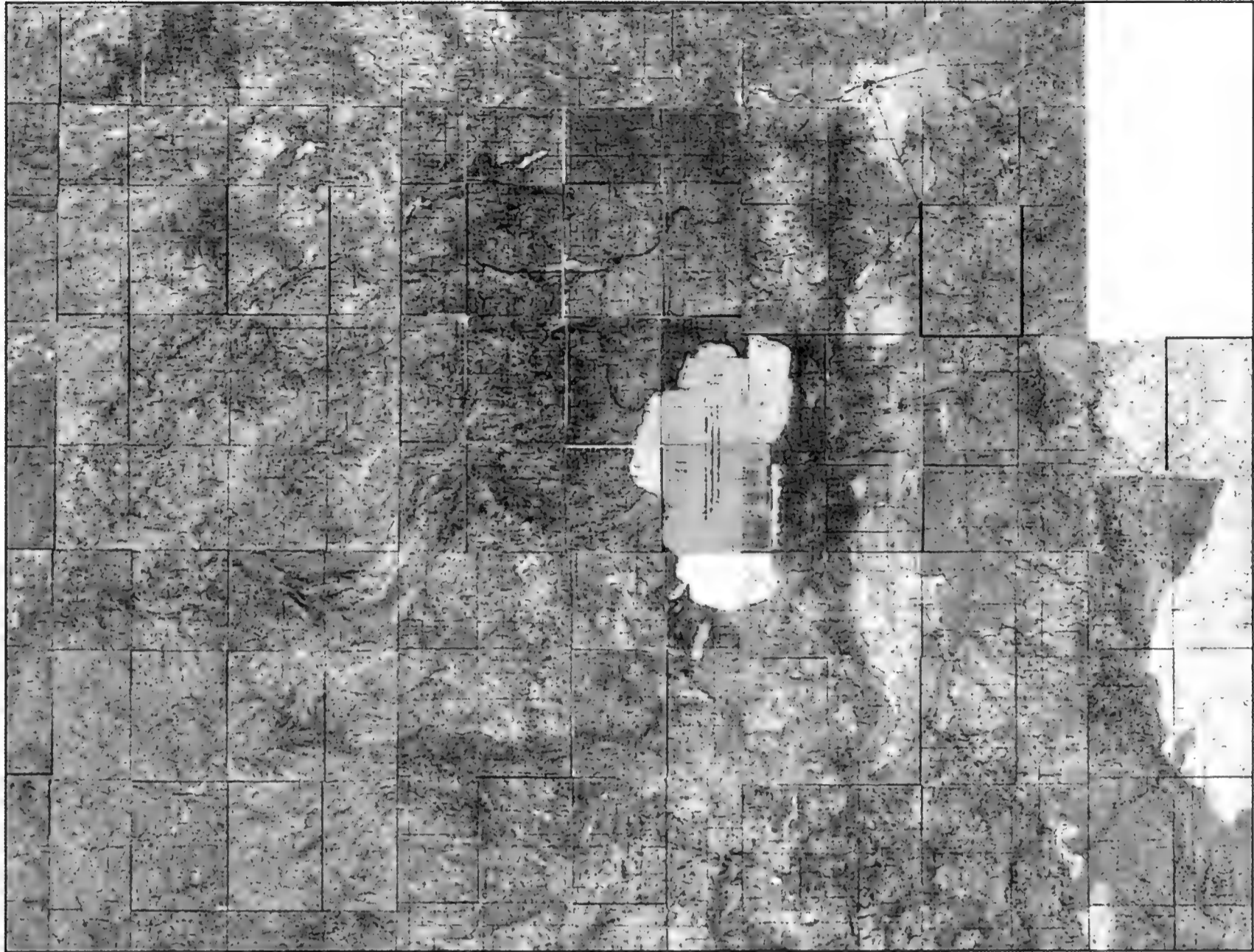
B

FIG. 6.   A mosaic of multiple VTM quadrangles representing the Lake Tahoe and Central Sierra Nevada region. Figure 6A shows the original maps. Figure 6B shows the GIS rendered from the VTMs, using WHR landcover types as the classification (Fig. 7).
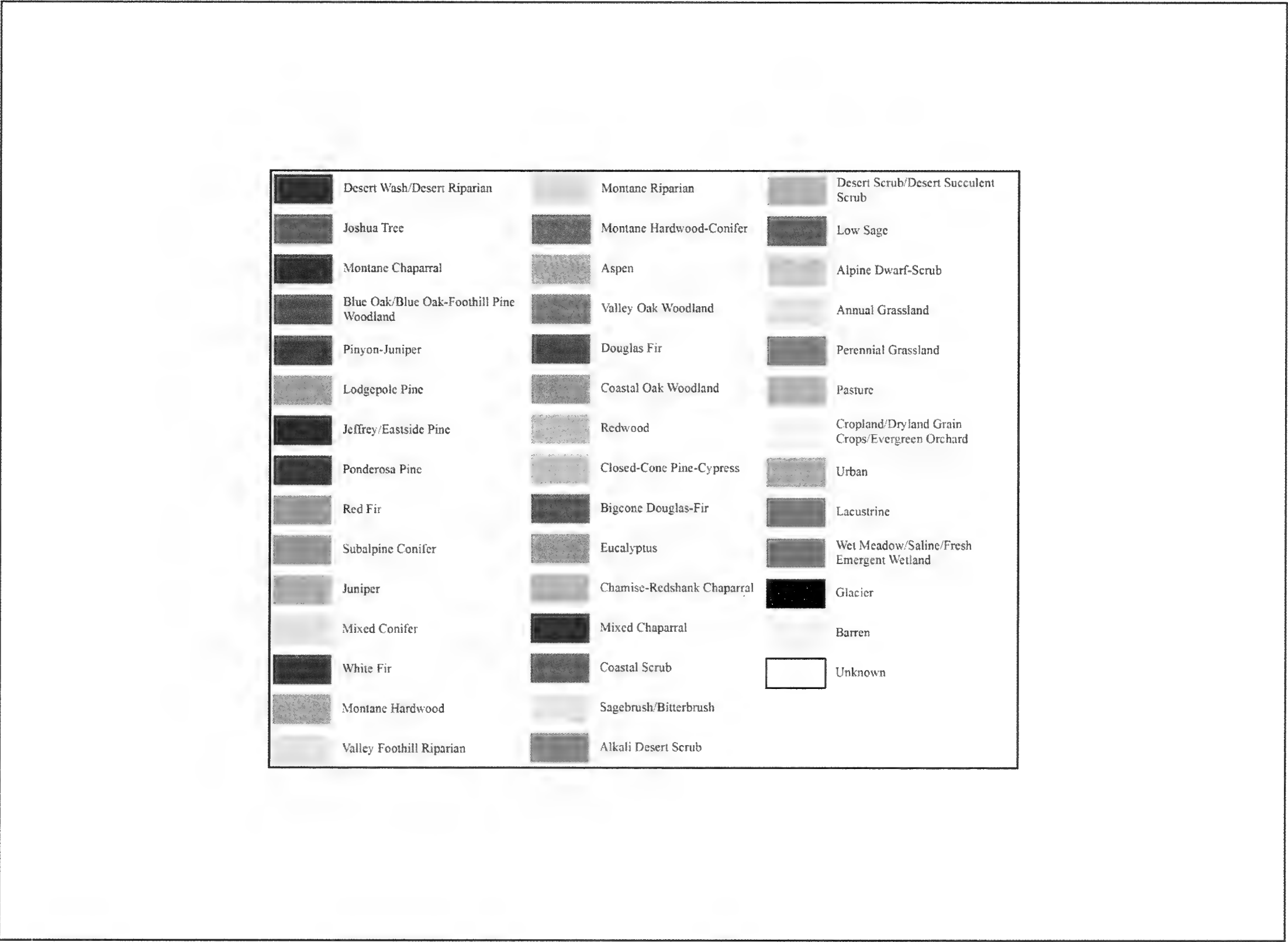
FIG. 7. The legend of the WHR types shown in the GIS portrayal of Figure 6.

FIG. 8. A detail of VTM map from the south shore of Lake Tahoe, from a movie that uses the VTMs to help inform changes in forest lands in the Sierra Nevada (Thorne & McQuinn 2012)

FIG. 9.   A detail from mosaicked VTM tiles from the Monterey Bay Area.

efforts. The first edition of the US GAP analysis program map for California (Davis et al 1995, 1998) has more species-specific information in it than other national products, which include a second edition National GAP Analysis effort (http://gapanalysis. usgs.gov/), Landfire (http://landfire.cr.usgs.gov/ viewer/), and NatureServe's (http://www. natureserve.org/) maps. However, even the state's MCV maps, which contain by far the most species-specific information among contemporary maps, do not retain at the polygon level the number of species recorded by the VTMs. In addition, while the MCV classification of landscapes has been adopted by the National Park Service, which has funded such mapping for all NPS lands in California, the methods are intensive, and despite a long-term dedicated effort, less than ½ the state has been mapped using this approach. The MCV rate of mapping is not dissimilar to the rate the VTM project accomplished, of about one half of the state in about 14 years. By recording the dominant species in each polygon, the VTMs have greater flexibility to be classed according to various classifications, for comparison to modern maps. Inclusion of this level of taxonomic detail could become a goal for contemporary mapping efforts.

Use of national-scale map classifications for assessment of landcover change in California may be problematic, because of the lack of recognition of endemic dominant tree species, and also due to widespread mis-identification or mis-classification of vegetation types, particularly of the second edition US GAP analysis survey map, and also of early versions of NatureServe's map for the region. While a formal comparative analysis of all contemporary map products available has not yet been done, the high levels of plant species diversity in California require some engagement of local botanists to develop maps sufficiently accurate for use in assessment of landcover change (Thorne et al 2008). It should be noted that the groups engaged with the different state-level mapping approaches are aware of each other's work, and are collaborating in an attempt to improve the quality of statewide maps.

The VTM maps can be used for several types of analysis. First, as shown by Griffin and Critchfield (1972), the ranges and locations of individual species can be developed. Second, assessment of change in the location of habitats can be determined (Thorne et al. 2008). However, the VTM polygons are generally too large to permit direct comparison with the more detailed maps produced using the MCV methodology, and for practical purposes, landcover change has so far been done using the state's more general classification system, the WHR.

Finally, several quadrangles that we suspect were surveyed are missing from the overall collection. Historically, it was permitted that originals were removed for use by various research and agency personnel. During the efforts to digitize the collection, several repositories of maps were recovered.

However, two 15' quadrangles are missing from the Central Coast ecoregion, which if recovered would improve representation for that region: quads 86B (west of Orestimba Peak) and 85D (south of the Mt. Doug and west of the Gilroy Hot Springs quadrangles). Additionally the 30' Cuyama quadrangle is missing a portion (156D tiles 3 and 4), and three 7.5' quadrangles south of Pacifico Mountain and San Fernando (162q, r, and w) were not in the collection. It may be possible that these quadrangles are still in existence, and the authors request agency and research personnel to search their archives. The VTM maps and corresponding GIS are posted on the VTM website at UC Berkeley (http://vtm. berkeley.edu), which can be used for further detail about the missing quadrangles and to obtain the data for other purposes. Additionally, two 30' quadrangles representing the locations of VTM plots around northern Lake Tahoe and to the west of it (the Colfax and Truckee quadrangles) would greatly improve the collection if they are found and returned.

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APPENDIX 1

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APPENDIX 2

The data fields in the VTM GIS. This Appendix provides a definition for each field found in the attribute tables of GIS developed from the VTMs. They are presented in descending order, which follows the column headings from left to right.

FID = internal GIS ID

VTM ID = unique polygon ID

VTM Quad ID = ?

Area HA = calculated polygon area in hectares

Area M^2 = calculated area in square meters

WHR1 = California Wildlife Habitat Relationship Code for primary vegetation type, derived from cross walking the Manual of California Vegetation (1995) classification to the WHR system.

WHR1 Type = Full name of the California Wildlife Habitat Relationship type for primary vegetation type, derived from cross walking the Manual of California Vegetation (1995) classification to the WHR system.

WHR2 = California Wildlife Habitat Relationship Code for secondary vegetation type, derived from cross walking the Manual of California Vegetation (1995) classification to the WHR system.

WHR2 Type = Full name of the California Wildlife Habitat Relationship type for secondary vegetation type, derived from cross walking the Manual of California Vegetation (1995) classification to the WHR system.

MCV1 1995 = Alliance name from 1995 edition of the Manual of California Vegetation. This is for the primary vegetation type in a polygon.

MCV2 1995 = Alliance name from 1995 edition of the Manual of California Vegetation. This is for the secondary vegetation type in a polygon.

MCV1 2009 = Alliance name from 2009 edition of the Manual of California Vegetation. This is for the primary vegetation type in a polygon.

MCV2 2009 = Alliance name from 2009 edition of the Manual of California Vegetation. This is for the secondary vegetation type in a polygon.

SP1–Sp9 = VTM codes listing the species, or occasionally the vegetation or land cover type, recorded in each polygon

SP1 Name–SP9 Name = Latin binomial for the species codes from previous column, from the first edition Jepson Manual (Hickman 1993).

CH Angle = Angle of cross-hatching in polygons that show cross-hatching. These lines refer to sparse vegetation or recent disturbance for the polygon in question. The disturbance can be either due to fire or to logging. If the cross-hatching is in black ink it refers to sparse vegetation, in red to brown ink (refer to scanned images, not completely recorded in GIS) it refers to fire, if in blue ink it refers to logging.

Note that for burned areas, the field instructions (Wieslander et al. 1934) indicate that crews were to get fire maps from local rangers and then to adjust the fire perimeters when in the field. Therefore, early fires recorded in the VTMs may represent more accurate fire boundaries than early fire boundaries derived from other sources. These fire boundaries may portrayed in a compiled form in the Weeks et al. (1943) publication for the central and northern Sierra Nevada, but they could also be extracted from the GIS of the VTMs to compare with other maps of fire perimeters from the 1930's, and comparison to contemporary fire perimeters.

We interpret the cross-hatching angles to mean the following (as per the field manual by Coffman (1934):

Burns

//: 45° angle. Recent burns are indicated by a cross-hatching of diagonal lines running from left to right in red to brown ink.

=: 90° angle. Brushfields and woodland areas which have resulted from fire within the virgin stands that are not restocking to coniferous timber. The timber species are present as reproduction, rather than as mature trees. (no visible reproduction). Indicated by cross-hatching of horizontal lines.

0 = no cross-hatching.

\\:135° angle. Brushfields and woodland areas which have resulted from fire within the virgin stands that are restocking to coniferous timber. The timber species are present as reproduction, rather than as mature trees. Numbers on top of the cross hatching refer to 1 = well stocked; 2 = medium stocked, and 3 = poorly stocked.

||: 360° angle. Areas recently deforested by burns, which have not yet developed into brushfields or other non-coniferous fire types. Indicated by cross-hatching of vertical lines.

Logging

//: 45° angle. Selectively logged areas with residual stand sufficient to justify a second cut prior to maturity of reproduction. Indicated by a cross-hatching of diagonal lines running from left to right;

=: 90° angle. Clean cut or burned logged over areas which are not restocking (no visible reproduction). Indicated by cross-hatching of horizontal lines.

\\:135° angle. Clean cut areas, which are restocked to seedlings, saplings, or trees. Numbers on top of the cross hatching refer to 1 = well stocked; 2 = medium stocked, and 3 = poorly stocked.

CH Color = the colors of cross-hatching were sometimes recorded during digitization, but could be added for all cross-hatching, using the scheme for cross-hatching above.

Vegstring = A compilation of the species names from the polygon and the crosshatching. This was used to determine the MCV type, from which WHR types were derived. Early

seral stage from cross-hatching was taken into account at this point.

Comments = Comments relating to species that may be out of the known range, uncertain codes, or other details related to that polygon.

CalVeg1 = A placeholder column in case the US Forest Service desires to translate the MCV types to CalVeg codes. This is for the primary type in the polygon.

CV1 Name = A placeholder column in case the US Forest Service desires to translate the MCV types to CalVeg names. This is for the primary type in the polygon.

CalVeg2 = A placeholder column in case the US Forest Service desires to translate the MCV types to CalVeg codes. This is for the secondary type in the polygon.

CV2 Name = A placeholder column in case the US Forest Service desires to translate the MCV types to CalVeg names. This is for the secondary type in the polygon.

VTM color = The colors in the VTMs are tied to a classification scheme that relied on Dixon colored pencils (Dixon Ticonderoga Company, Lake Mary, FL) of different numbers. The colors refer to categories of land cover and vegetation. There are extensive notes about the composition of species related to the colors in the field manuals. We did not determine a way to process the colors (which may or may not be consistently applied to all maps, there are certain maps such as the southern-most quads in north coast ecoregion which have different coloring). Remote sensing techniques might be applied to the scans if review of the field manuals suggests that better vegetation types could be defined using the colors than the approach we used. We used the actual species recorded, in addition to any cross-hatching to assign a MCV alliance name. We checked to see if the color of the polygon indicated a landcover type in agreement to the one we assigned. The color in some cases caused us to change a hardwood woodland type to a chaparral type.

VTM type = This is associated the color discussion above, and could be filled out later if found useful.

Vetting = This indicates if species listed in the polygon were checked in one of the several levels of vetting, and if so for what region of the state.

APPENDIX 3. The root mean square error (RMSE), and notes for each VTM quadrangle that was digitized. These values represent the degree to which the basemaps that the vegetation polygons are drawn on differ from the current measure of topography, and are obtained by registering the old topography to a modern topographic surface. In essence, these measurements provide an estimate of potential spatial error in the location of vegetation introduced by the maps it was recorded upon. Note that some 15' and 7.5' quadrangles that either were not used in the final GIS or were not registered are listed, in order to provide a full set of VTM quadrangle codes. Where RMSE rows are marked with a "—" indicates that the value was not recorded. Generally single numbers identify a 30' quadrangle, a number followed by a capital letter indicate a 15' quadrangle, and a number followed by a lowercase letter signifies a 7.5' quadrangle. Many of the 7.5' quadrangles are also represented in 15' or 30' maps, in which case the 7.5' were not included in the GIS, and RMSE was not tested because we assumed the 7.5' versions were copied from the coarser scale maps. However, those 7.5' quadrangles were scanned.

VTM quadrangle number	Quadrangle name	Root mean square error (m)	Quadrangle size, in minutes	Extent of quadrangle surveyed — 100 percent if blank	Notes made during digitization
7	SEIAD VALLEY	131.6	30		
8	PRESTON PEAK	116.5	30		
12	SAWYERS BAR	86.1	30		
22	BURNEY	114.2	30		
23	REDDING	80.4	30		
24	WEAVERVILLE	119.1	30		
25	BIG BAR	127.8	30	approx. 50%	lower left section missing
30	SPORTSHAVEN	80.4	30	approx. 50%	C&D apparently missing
33	SHINGLETOWN	77.7	30	approx. less than 50%	quads only partially mapped
37	SIERRAVILLE	118.7	30		
38	DOWNIEVILLE	129.5	30		
39	KIMSHEW POINT	189.6	30		
40	CHICO	139.3	30		
49	BUTTE CITY	31.0	30		
50	SMARTVILLE	180.3	30		
51	COLFAX	115.8	30		
52	TRUCKEE	106.2	30	over 50%	lower right quad missing
53	WELLINGTON	94.4	30		
54	MARKLEEVILLE	127.7	30		
55	PYRAMID PEAK	83.7	30		
56	PLACERVILLE	119.7	30		
57	SACRAMENTO EAST	137.4	30		
65	NAPA	78.8	30		
68	JACKSON	73.5	30		
69	DEVILS NOSE	106.6	30	fully mapped. I think it its fine	Note on quad — topography in fairly large error in section B5
70	DARDANELLE	85.6	30		
71	BRIDGEPORT	48.1	30		
76	MT. LYELL	72.7	30		
77	YOSEMITE FALLS	83.1	30		
78	SONORA	160.9	30		
84	HALF MOON BAY	63.3	30		
89	MARIPOSA	71.3	30	approx. less than 50%	The northwest corner of this set is missing
90	KAISER PEAK	108.1	30	approx. less than 50%	Upper right and lower right quads missing. Partial veg polys.
91	MT. GODDARD	50.8	30	approx. less than 50%	partial VM polys
98	MOUNT WHITNEY	75.5	30	approx. less than 50%	partial polys on the lower left quad; scale is suspect
99	TEHIPITE DOME	59.3	30	approx. 50%	Upper left & right quads on same canvas backing.
100	PATTERSON MTN.	48.4	30		
103	PANOCHE	68.6	30	approx. 50%	legends in margins, partial VTM polys

APPENDIX 3. CONTINUED

VTM quadrangle number	Quadrangle name	Root mean square error (m)	Quadrangle size, in minutes	Extent of quadrangle surveyed — 100 percent if blank	Notes made during digitization
108	PRIEST VALLEY	51.7	30		
109	COALINGA	73.9	30	approx. 75%	upper right quad missing, legends in margins
112	KAWEAH	72.7	30	approx. 50%	lower right missing, partial polys, no legends
113	OLANCHA	77.2	30	approx. less than 50%	partial polys, no legend
125	KERNVILLE	52.2	30		
128	LOST HILLS	83.5	30		
129	CHOLAME	81.5	30		
134	MCKITTRICK SUMMIT	74.2	30		
135	BUENA VISTA LAKE BED	97.6	30		only a few polys
136	BRECKENRIDGE MTN.	124.2	30		
137	MOJAVE	82.8	30	a little over 50	partial polys, legends in margins and on maps, some edges cut
153	BISSELL	76.1	30		
154	LIEBRE TWINS	94.1	30		
155	PLEITO HILLS	65.1	30		
156	CUYAMA	100.9	30		D—3,4 missing
157	LOMPOC	77.2	30		
158	GUADALUPE	78.5	30	over 50%	only 2 quads for this coastal area, no legend
165	SAN GORGONIO MTN.	110.8	30		
174	INDIO	173.8	30	approx. less than 50%	only lower L&R quads available, mislabeled according to labeling scheme
175	SAN JACINTO	81.3	30		
176	LAKE ELSINORE	77.9	30		
177	CORONA NORTH	80.3	30		
180	SAN LUIS REY	70.6	30		
181	RAMONA	101.6	30		
182	RABBIT PEAK	101.3	30		
190	CARRIZO MTN.	175.8	30		
191	CUYAMACA PEAK	46.4	30		
179A	SAN CLEMENTE	70.6	30		
N59B	WADSWORTH	98.2	30	approx. less than 50%	upper and lower right quads missing, small amount of veg data. no data on B tiles, so not registered
N60	RENO	113.3	30		
N61	CARSON	128.9	30	over 50%	only lower right quad in collection got the others from Zinke 3/07
N62C	WABUSKA	92.6	30	approx. less than 50%	only lower left quad present, partial veg data in CA.
43A	COVELO EAST	46.8	15	over 50%	lower left cut out
43D	JAMISON RIDGE	51.3	15	approx. 50%	upper right cut off
46A	FOSTER MTN.	27.5	15	approx. less than 50%	US Army Corps Engineers basemap
46B	WILLITS	32.0	15	approx. less than 50%	only partial topo and veg coverage
46D	UKIAH	27.6	15		
47C	LAKEPORT	24.4	15		
47D	BARTLETT SPRINGS	24.4	15	approx. less than 50%	partial veg information

APPENDIX 3. CONTINUED

VTM quadrangle number	Quadrangle name	Root mean square error (m)	Quadrangle size, in minutes	Extent of quadrangle surveyed — 100 percent if blank	Notes made during digitization
59d	—	—	15		US Army Corps Engineers basemap, not used
60a	LOWER LAKE	9.5	15		
60b	KELSEYVILLE	224.5	15		US Army Corps Engineers basemap
61A	HOPLAND	29.9	15		
64A	SANTA ROSA	30.0	15	approx. less than 50%	veg map partial
64D	PETALUMA	31.3	15	over 50%	partial veg map
65C	MARE ISLAND	78.8	15		
65D	CORDELIA	78.8	15		
66B	ALLENDALE	20.6	15	over 50%	lower left edge cut off
66C	ANTIOCH NORTH	23.8	15		
72	—	—	15		
79A	COPPEROPOLIS	42.5	15		
80C	TRACY	34.0	15		
81A	BRENTWOOD	22.6	15		
81B	DIABLO	35.6	15		
81C	DUBLIN	31.3	15	over 50%	corners cut off
81D	ALTAMONT	30.7	15	over 50%	legends in margin, some edges cut
82A	OAKLAND EAST	34.6	15	over 50%	partial edges cut off
82B	SAN FRANCISCO NORTH	36.5	15		
82C	SAN MATEO	35.2	15		
82D	HAYWARD	67.9	15	over 50 fine	partial veg mapped, edges partially cut off
84A	PALO ALTO	63.3	15		
85A	MT. DAY	57.2	15		
85B	SAN JOSE EAST	57.2	15		
85C	—	57.2	15		
86A	ORESTIMBA PEAK	30.6	15		
86C	GILROY HOT SPRINGS	30.6	15	over 50%	edges cut
86D	PACHECO PASS	30.6	15	over 50%	edges cut
88A	INDIAN GULCH	22.2	15		
104A	QUIEN SABE VALLEY	23.3	15		
104B	—	23.0	15		
104C	—	27.9	15		
104D	SAN BENITO	27.8	15		
105A	—	46.7	15		
105B	SOQUEL	33.4	15		
105C	MONTEREY	45.5	15		
105D	SALINAS	40.2	15		
106A	CARMEL VALLEY	24.7	15		
106B	POINT SUR	21.7	15		
106D	PARTINGTON RIDGE	30.1	15		
107A	NORTH CHALONE PEAK	48.3	15		
107B	SOLEDAD	48.3	15		
107C	JUNIPERO SERRA PEAK	48.3	15	over 50%	2 maps this one edition of 1930, partial polys
107D	THOMPSON CANYON	48.3	15		
130A	SAN MIGUEL	91.3	15		
130B	BRADLEY	57.7	15		
130C	ADELAIDA	41.0	15		
130D	PASO ROBLES	46.7	15		
131A	BRYSON	44.0	15		
131B	CAPE SAN MARTIN	33.9	15		
131C	PIEDRAS BLANCAS	30.0	15	over 50%	mostly water quad
131D	SAN SIMEON	30.3	15	over 50%	mostly water quad
132A	SAN LUIS OBISPO	65.8	15		
132B	CAYUCOS	37.4	15		
132C	PORT SAN LUIS	49.4	15		
132D	ARROYO GRANDE NE	54.0	15		

APPENDIX 3. CONTINUED

VTM quadrangle number	Quadrangle name	Root mean square error (m)	Quadrangle size, in minutes	Extent of quadrangle surveyed — 100 percent if blank	Notes made during digitization
133A	LA PANZA	30.2	15		
133B	POZO SUMMIT	32.1	15		
133C	NIPOMO	29.9	15		
133D	LOS MACHOS HILLS	30.6	15		
159A	SANTA BARBARA	58.2	15	over 50%	only part of lands around SB are mapped on this quad
159B	GOLETA	58.2	15	over 50%	only part of lands around Goleta are mapped on this quad
160A	SANTA PAULA	61.7	15		
160B	VENTURA	61.7	15		
160D	CAMARILLO	61.7	15		
161A	NEWHALL	37.8	15		
161B	PIRU	74.8	15		
161C	TRIUNFO PASS	Not tested	15		
161D	CALABASAS	59.9	15		
162A	PACIFICO MOUNTAIN	141.5	15		
162B	SAN FERNANDO	141.5	15		
162D	PASADENA	141.5	15		
163A	MOUNT SAN ANTONIO	157.1	15	over 50%	there are 2 maps, each with 1/2 the veg polys
163B	VALYERMO	157.1	15		
163C	GLENDORA	157.1	15		
163D	CUCAMONGA PEAK	157.1	15		
164C	SAN BERNARDINO NORTH	60.3	15		
164D	REDLANDS	60.3	15		
178A	LONG BEACH	52.0	15	approx. less than 50%	small area mapped, legend in margin
178B	REDONDO BEACH	52.0	15	approx. 50%	partial veg polys
178C	SAN PEDRO	52.0	15		
178D	SEAL BEACH	52.0	15		
192A	LA JOLLA	30.9	15		
192D	NATIONAL CITY	30.9	15	over 50%	map extends beyond box, edges cut, good condition
40d	RICHARDSON SPRINGS NW	—	n/a		
40f	RICHARDSON SPRINGS	—	n/a		
40k	CHICO	—	n/a		
40l	ORD FERRY	—	n/a		
40m	LLANO SECO	—	n/a		
40p	OROVILLE	—	n/a	over 50%	upper left cut off
49a	PALERMO	—	7.5		Upper right and lower left cut off
49b	BIGGS	—	7.5		
49c	WEST OF BIGGS	—	7.5		
49d	BUTTE CITY	—	7.5		
49E	MARYSVILLE BUTTES	—	n/a		This quad may have high RMSE.
49f	PENNINGTON	—	7.5		
49g	GRIDLEY	—	7.5		
49h	HONCUT	—	7.5		
49i	YUBA CITY	—	7.5		
49j	SUTTER	—	7.5		
49k	SUTTER BUTTES	—	7.5	approx. 50%	Contour level 5 feet, between broken contours 500 feet.
49l	MERIDIAN	—	7.5		
49m	GRIMES	—	7.5		
49n	TISDALE WEIR	—	7.5		
49o	GILSIZER SLOUGH	—	7.5		

APPENDIX 3. CONTINUED

VTM quadrangle number	Quadrangle name	Root mean square error (m)	Quadrangle size, in minutes	Extent of quadrangle surveyed — 100 percent if blank	Notes made during digitization
49p	OLIVEHURST	—	7.5		
50e	LOMA RICA	—	7.5	over 50%	upper right corner cut off, but present, incomplete topo and veg work
50m	WHEATLAND	—	7.5		
57c	LINCOLN	137.4	n/a		Values for this series from the 30′ quad.
57d	SHERIDAN	137.4	7.5		
57e	PLEASANT GROVE	137.4	7.5		
57f	ROSEVILLE	137.4	7.5		
57j	FOLSOM	137.4	7.5	over 50%	map not glued to canvas, entire. Only partial topo and veg coverage
57k	CITRUS HEIGHTS	137.4	7.5		
57l	RIO LINDA	137.4	7.5		
57n	CARMICHAEL	137.4	7.5		
67a	CARBONDALE	40.5	7.5		
67h	GOOSE CREEK	—	7.5		
67i	CLEMENTS	—	7.5		
67p	LINDEN	—	7.5		
78l	LA GRANGE	—	7.5	over 50%	only partial topo and veg map
78m	SNELLING	—	7.5		
78n	MERCED FALLS	—	7.5	over 50%	only partial topo and veg map
80o	WESTLEY	37.8	7.5	approx. less than 50%	partial veg mapped, legends in margin
79c	BACHELOR VALLEY	42.5	7.5	approx. less than 50%	only partial veg
79d	FARMINGTON	42.5	7.5	approx. less than 50%	very small amount of veg
79f	OAKDALE	42.5	7.5		
79i	COOPERSTOWN	42.5	7.5	approx. less than 50%	partial veg mapped
79p	TURLOCK LAKE	42.5	7.5	approx. less than 50%	partial veg mapped
80o	WESTLEY	37.8	n/a	approx. less than 50%	partial veg mapped, legends in margin
87a	WINTON	22.2	7.5		Old Quadrangle name
88c	HAYSTACK MOUNTAIN	22.2	7.5		Old Quadrangle name
88d	YOSEMITE LAKE	22.2	7.5	approx. less than 50%	very small amount of veg mapped
88f	PLANADA	22.2	7.5	approx. less than 50%	partial veg mapped, legend
88i	RAYNOR CREEK	22.2	7.5	approx. less than 50%	very small amount of veg mapped
88j	LE GRAND	22.2	7.5	approx. less than 50%	very small amount of veg mapped
101a	—	31.4	7.5		
111a	—	—	7.5		
111h	ROCKY HILL	56.2	7.5	approx. 50%	no polys in the flats
162m	LA CRESENTA	141.5	7.5		Old Quadrangle name
162n	SUNLAND	141.5	7.5		Old Quadrangle name
162o	PACOIMA	141.5	7.5		Old Quadrangle name
162p	VAN NUYS	141.5	7.5	approx. 50%	about 1/2 of map has veg polys; old quadrangle name
162s	ALTADENA	141.5	7.5		Old Quadrangle name
162t	SIERRA MADRE	—	7.5	approx. 50%	a few veg polys
162u	EL MONTE	—	7.5	approx. less than 50%	legend in map, partial polys; old quadrangle name

APPENDIX 3. CONTINUED

VTM quadrangle number	Quadrangle name	Root mean square error (m)	Quadrangle size, in minutes	Extent of quadrangle surveyed — 100 percent if blank	Notes made during digitization
162v	ALHAMBRA	—	7.5	approx. 50%	partial polys, legend on margin; old quadrangle name
162x	HOLLYWOOD	141.5	7.5	approx. less than 50%	mostly city; old quadrangle name
162y	SAWTELLE	141.5	7.5		Old Quadrangle name
163p	AZUSA	—	7.5		Old Quadrangle name
163q	GLENDORA	—	7.5	approx. 75%	about 1/2 of map has veg polys and topo lines; ; old quadrangle name
163r	LA VERNE	—	7.5	approx. 75%	partial polys; old quadrangle name
163w	CLAREMONT	—	7.5	approx. less than 50%	partial polys, legend on map; ; old quadrangle name
163x	COVINA	—	7.5		Old Quadrangle name
163y	PUENTE	—	7.5		Old Quadrangle name
177d	LA BREA	—	n/a	approx. 50%	1/2 of map has polys
177e	LA HABRA	52.0	7.5	approx. less than 50%	bounding box coordinates cut off, check against other maps. Partial polys; old quadrangle name
178d	INGLEWOOD	—	n/a	approx. less than 50%	partial veg polys; old quadrangle name

APPENDIX 4. The list of all codes and the names assigned to them in the VTM map data. Codes with parentheses around the species name indicate the entity was dead.

Species code	Species and land cover name used
***	No data
A	*Quercus agrifolia*
A2	*Alnus rhombifolia*
A3	*Populus tremuloides*
Aa	*Amelanchier alnifolia*
Aaa	*Arctostaphylos auriculata*
Aan	*Arctostaphylos andersonii*
Aap	*Arctostaphylos pechoensis*
Aar	*Artemisia arbuscula*
Ab	*Xylococcus bicolor*
Abm	*Abronia maritima*
Ac	*Artemisia californica*
Aca	*Amorpha californica*
Acg	*Acer glabrum*
Acl	*Acleisanthes longiflora*
Acm	*Achyrachaena mollis*
Acn	*Arctostaphylos canescens*
Aco	*Arctostaphylos columbiana*
Acp	*Acaena pinnatifida californica*
Acs	*Acamptopappus sphaerocephalus*
Ad	*Arctostaphylos pringlei drupacea*
Ado	*Adolphia californica*
Adr	*Artemisia dracunculus*
Ae	*Arctostaphylos manzanita elegans*
Aec	*Aesculus californica*
Af	*Adenostoma fasciculatum*
Aff	*Atriplex confertifolia*
Afr	*Amorpha fruticosa*
Ag	*Arctostaphylos glauca*
Agc2	*Elymus caninus*
Agl	*Arctostaphylos glandulosa*
Agr	*Acacia greggii*
Ags2	*Pseudoroegneria spicata spicata*
Ah	*Arctostaphylos hookeri*
Airpt	Airport
Alo	*Allenrolfea occidentalis*
Am	*Arctostaphylos manzanita*
Ama	*Arctostaphylos viscida mariposa*
Ame	*Aster chilensis*
Amr	*Arctostaphylos morroensis*
Amy	*Arctostaphylos myrtifolia*
An	*Arctostaphylos nevadensis*
Ane	*Arctostaphylos nevadensis*
Ang	*Antirrhinum multiflorum*
Ani	*Arctostaphylos nissenana*
Ann	Annuals
Ao	*Arctostaphylos otayensis*
Aob	*Arctostaphylos obispoensis*
Ap	*Arctostaphylos patula*
Apa	*Artemisia tridentata parishii*
Apc	*Apocynum cannabinum*
Apc2	*Aira caryophyllea*
Ape	*Arctostaphylos pechoensis*
Api	*Arctostaphylos pilosula*
Apm	*Arctostaphylos pumila*
App	*Arctostaphylos patula*
Aps	*Arctostaphylos mewukka mewukka*
Apu	*Arctostaphylos pungens*
Apy	*Arctostaphylos parryana*
Ar	*Arctostaphylos rudis*
Ar2	*Agrostis variabilis*

Species code	Species and land cover name used
Arc	*Artemisia cana bolanderi*
Are	*Arctostaphylos regismontana*
Arr	*Artemisia rothrockii*
Arsp	*Artemisia spinescens*
As	*Adenostoma sparsifolium*
Asa	*Actaea rubra*
Asbo	*Astragalus bolanderi*
Asc	*Asclepias cordifolia*
Ase	*Arctostaphylos nummularia*
Asi	*Arctostaphylos silvicola*
Asl	*Aster chilensis*
Aso2	*Aristida oligantha*
Asp	*Atriplex spinifera*
Ast	*Arctostaphylos stanfordiana*
At	*Arctostaphylos tomentosa*
Atb	*Atriplex lentiformis breweri*
Atc	*Atriplex canescens*
Ate	*Alnus incana tenuifolia*
Atem	*Artemisia* sp.
Atex	*Atriplex argentea mohavensis*
Atl	*Atriplex lentiformis*
Ato	*Artemisia nova*
Atp	*Atriplex polycarpa*
Atr	*Artemisia tridentata*
Atri	*Artemisia tridentata*
Att	*Atriplex lentiformis torreyi*
Atx	*Atriplex* sp.
Aty	*Artemisia pycnocephala*
Av	*Arctostaphylos viscida*
Avb	*Avena barbata*
Avb2	*Avena barbata*
Avf2	*Avena fatua*
Avh	*Artemisia douglasiana*
Avh2	*Artemisia vulgaris heterophylla*
Avx2	*Avena* sp.
Aw	*Arctostaphylos wieslanderi*
Ax	*Astragalus* sp.
Axp	*Arctostaphylos* sp.
Ay	*Arctostaphylos* sp.
B	*Quercus kelloggii*
B1	*Abies bracteata*
B3	*Populus balsamifera trichocarpa*
Ba	Barren
Bas2	*Bassia hyssopifolia*
Bc	*Brickellia californica*
Bd	*Baccharis douglasii*
Be	*Baccharis emoryi*
Beach	Beach
Ber	*Berberis aquifolium repens*
Bf	*Berberis fremontii*
Bg	*Brickellia grandiflora*
Bg2	*Bromus grandis*
Bh	*Bromus hordeaceus*
Bh2	*Bromus hordeaceus*
Bi	*Triteleia ixioides*
Bm2	*Bromus carinatus carinatus*
Bma2	*Bromus madritensis*
Bn	*Berberis nervosa*
Bp	*Baccharis pilularis*
Br2	*Bromus diandrus*
Bra2	*Bromus hordeaceus*
Brm	*Brickellia microphylla*
Brm2	*Briza minor*

Species code	Species and land cover name used
Bru	*Bromus madritensis rubens*
Bru2	*Bromus madritensis rubens*
Brx	Unknown Code
Bs	*Pseudotsuga macrocarpa*
Bsg	*Balsamorhiza sagittata*
Bsp2	*Bromus* sp.
BT	*Sequoia gigantea*
Bt2	*Bromus tectorum*
Burn	Burn
Bv	*Baccharis salicifolia*
Bv2	*Bromus vulgaris*
Bx2	*Bromus* sp.
C	*Quercus chrysolepis*
C.Nev	*Cupressus nevadensis*
Ca	*Ceanothus foliosus foliosus*
Ca1	*Opuntia* sp.
CAG	Unknown Code
Cax	*Carex* sp.
Cb	*Cercocarpus betuloides*
Cc	*Ceanothus cuneatus*
Ccl	*Carpenteria californica*
Ccm	*Chrysolepis chrysophylla minor*
Cco	*Ceanothus cordulatus*
Ccr	*Ceanothus crassifolius*
Ccu	*Ceanothus cuneatus*
Ccx	Unknown Code
Cd	*Ceanothus leucodermis*
Cde	*Ceanothus dentatus*
Cdi	*Ceanothus diversifolius*
Cdu	*Cneoridium dumosum*
Ce	*Echinocereus engelmannii*
Cec	*Cercis occidentalis*
Cem	*Centaurea melitensis*
Ceme	Cemetary
Ceo	*Cephalanthus occidentalis californicu*
Cf	*Chamaebatia foliolosa*
Cfa	*Chamaebatia australis*
Cfo	*Ceanothus foliosus*
Cg	*Ceanothus greggii*
Cgp	*Ceanothus greggii perplexans*
Cgr	*Collomia grandiflora*
Chb	*Ericameria bloomeri*
Chc	*Chaenactis carphoclinia*
Chn	*Chrysothamnus nauseosus*
Chp	*Chrysothamnus parryi*
Chr	*Chrysothamnus* sp.
Chv	*Chrysothamnus viscidiflorus*
Chx	Unknown Code
Ci	*Ceanothus integerrimus*
Cim	*Ceanothus impressus*
Cin	*Ceanothus incanus*
Cj	*Ceanothus jepsonii*
Cl	*Cercocarpus ledifolius*
Cle	*Ceanothus lemmonii*
Clo	*Ceanothus* sp.
Cm	*Ceanothus megacarpus megacarpus*
Cn	*Cornus nuttallii*
Cnc	*Chrysothamnus nauseosus consimilis*
Cng	*Chrysothamnus nauseosus gnaphalodes*
Cno	*Chrysothamnus nauseosus albicaulis*
Co	*Ceanothus oliganthus*
Coa	*Convolvulus arvensis*
Cof	*Lessingia filaginifolia*

Species code	Species and land cover name used
Cog	*Coreopsis gigantea*
Col	*Calystegia occidentalis s.l.*
Coo	*Calystegia occidentalis*
Cp	*Pinus coulteri*
Cpa	*Ceanothus palmeri*
Cpl	*Ceanothus papillosus*
Cpo	*Ceanothus prostratus*
Cpr	*Ceanothus parryi*
Cpu	*Calochortus pulchellus*
Cpv	*Ceanothus parvifolius*
Cr	*Corylus cornuta californica*
Cra	*Coleogyne ramosissima*
Crc	*Croton californicus*
Crf	*Ceanothus fresnensis*
Cri	*Ceanothus cuneatus rigidus*
Crn	*Cryptantha intermedia*
Cs	*Chrysolepis sempervirens*
Csa	*Ceanothus sanguineus*
Cse	*Ceanothus prostratus*
Cso	*Ceanothus oliganthus sorediatus*
Csp	*Ceanothus spinosus*
Ct	*Ceanothus thyrsiflorus*
Ctc	*Ceanothus thyrsiflorus*
Ctl	*Ceanothus tomentosus olivaceus*
Cto	*Ceanothus tomentosus*
Cu	Cultivated
Cv	*Ceanothus velutinus*
Cve	*Ceanothus verrucosus*
Cvp	*Chrysothamnus viscidiflorus puberulus*
Cx	*Ceanothus* sp.
Cxb	*Carex barbarae*
Cy	*Cycladenia humilis*
D	*Pseudotsuga menziesii menziesii*
D'	*Quercus douglasii*
D3	*Fraxinus anomala*
Da	*Mimulus aurantiacus*
Dam	*Datura wrightii*
Dc	*Dicentra chrysantha*
De	Desert
Deser	Desert
Dis2	*Distichlis spicata*
DIt2	*Distichlis spicata*
DLake	Dry Lake
Dp	*Pinus sabiniana*
Dpu	*Mimulus aurantiacus puniceus*
Dr	*Dendromecon rigida*
Dump	Dump
Dy	*Cupressus sargentii*
E	*Quercus engelmannii*
Ea	*Encelia actoni*
Ear	*Ericameria arborescens*
Eb	*Ericameria brachylepis*
Eba	*Eriogonum baileyi*
Ec	*Eriodictyon californicum*
Eca	*Ephedra californica*
Ech	*Eucrypta chrysanthemifolia chrysanthemifolia*
Ech2	*Ellisia chrysanthemifolia*
Eci	*Erodium cicutarium*
Eci2	*Erodium cicutarium*
Eco	*Eriophyllum confertiflorum*
Eco2	*Elymus condensatus*
Ecr	*Eriodictyon crassifolium*
Ecs	*Ericameria cuneata spathulata*

Species code	Species and land cover name used
Ecu	*Ericameria cuneata*
Ed	*Eriogonum deflexum*
Ee	*Ericameria ericoides*
Eel	*Eriogonum elatum*
Ef	*Eriogonum fasciculatum*
Efa	*Marah fabacea*
Efc	*Eriogonum cinereum*
Eff	*Eriogonum fasciculatum foliolosum*
Efp	*Eriogonum fasciculatum polifolium*
Ehe	*Eriogonum heermannii*
Em	*Euphorbia misera*
Em2	*Elymus* X trachycaulus
Emi	*Eriogonum microthecum*
Eml	*Eriogonum microthecum*
Emo	*Ericameria cooperi cooperi*
Emp	*Emmenanthe penduliflora*
En	*Eriogonum nudum*
Enc	*Encelia californica*
Ene	*Ephedra nevadensis*
Enf	*Encelia farinosa*
Ep	*Eriogonum parvifolium*
Epa	*Ericameria palmeri*
Epc	*Epilobium ciliatum*
Epi	*Ericameria pinifolia*
Epv	*Ephedra viridis*
Era	*Eriogonum arborescens*
Erc	*Ericameria cooperi cooperi*
Erd	*Eriogonum douglasii douglasii*
Ere	*Eriogonum elongatum elongatum*
Ero	*Erodium botrys*
Es	*Picea engelmannii*
Esa	*Eriophyllum staechadifolium*
Esc	*Eschscholzia californica*
Ese	*Eremocarpus setigerus*
Esp	*Erodium* sp.
Et	*Eriodictyon trichocalyx*
Etl	*Eriodictyon trichocalyx lanatum*
Eto	*Eriodictyon tomentosum*
Eu	*Eucalyptus* sp.
Euc	*Camissonia californica*
Eul	*Krascheninnikovia lanata*
Eum	*Eriogonum umbellatum*
Ev	*Eriogonum roseum*
Evm	*Eriogonum luteolum*
Ew	*Eriogonum wrightii*
Ex	*Eriogonum* sp.
F3	*Populus fremontii fremontii*
Far2	*Festuca* sp.
Fbi	*Ambrosia chamissonis*
Fc	*Fremontodendron californicum*
Fca	*Fragaria vesca*
Fch	*Ambrosia chenopodiifolia*
Fco	*Festuca* sp. *viridula*
Fd	*Fraxinus dipetala*
Fg	*Frankenia salina*
Fm2	*Vulpia myuros hirsuta*
Fmv2	*Vulpia myuros myuros*
Fnm	*Forestiera pubescens*
Fp	*Pinus balfouriana*
Fr2	*Festuca* sp. *rubra*
Fra	*Ambrosia acanthicarpa*
Fx2	*Festuca* sp.
G	*Quercus garryana*

Species code	Species and land cover name used
G1	*Abies grandis*
Gb	*Gnaphalium canescens beneolens*
Gd	*Gayophytum diffusum*
Ge	*Garrya elliptica*
Gf	*Garrya fremontii*
Gfb	*Garrya buxifolia*
Gfl	*Garrya flavescens*
Gfv	*Garrya congdonii*
Gh	*Gaultheria humifusa*
Gl	*Gutierrezia microcephala*
Glaci	Glacier
Gls	*Glossopetalon spinescens*
Gr	Grass sp.
Gr2	Grass sp.
Grs	*Grayia spinosa*
Gs	*Gaultheria shallon*
Gsa	*Gutierrezia sarothrae*
Gv	*Garrya veatchii*
Gy	*Cupressus goveniana*
H	*Tsuga heterophylla*
H'	Unknown Code
H2	*Aesculus californica*
Hb	Herbs
Hb2	Herbs
Hd	*Holodiscus discolor*
Hdd	*Holodiscus discolor*
Hdg	*Holodiscus microphyllus glabrescens*
Hg	*Heterotheca grandiflora*
Hg2	*Hordeum marinum gussoneanum*
Hgr	*Helianthus gracilentus*
Hgu2	*Hordeum marinum gussoneanum*
Hj2	*Hordeum jubatum*
Hm	*Tsuga mertensiana*
Hm2	*Hordeum murinum*
Hp	*Hypericum perforatum*
Hp2	*Hypericum perforatum*
Hpe	*Helianthus petiolaris petiolaris*
Hs	*Hazardia squarrosa*
Hsc	*Helianthemum scoparium*
Hsv	*Helianthemum scoparium*
Hys	*Hymenoclea salsola*
I	*Calocedrus decurrens*
Ia	*Isomeris arborea*
Iax	*Iva axillaris robustior*
Imi	*Iris missouriensis*
Iv	*Isocoma acradenia acradenia*
Ivv	*Isocoma menziesii vernonioides*
J	*Pinus jeffreyi*
J3	*Juncus* sp.
Jc	*Juniperus californica*
Jm	*Juniperus communis*
Jo	*Juniperus occidentalis*
Ju	*Juniperus osteosperma*
Jue	*Juncus effusus*
Jx	*Juncus* sp.
K	*Pinus attenuata*
Kc2	*Koeleria macrantha*
Koa	*Kochia americana*
L	*Pinus contorta murrayana*
L'	*Umbellularia californica*
La	*Lupinus albifrons*
Laf	*Lithophragma affine*
Lake	Water

Species code	Species and land cover name used
Lal	*Lupinus albicaulis*
Lar	*Lupinus arboreus*
Lc	*Pinus contorta*
Lcf	*Leptodactylon californicum*
Lch	*Lupinus chamissonis*
Lde	*Lithocarpus densiflorus echinoides*
Lg	*Ledum glandulosum*
Lig	*Ligusticum grayi*
Lm2	*Lolium multiflorum*
Ln	*Lepidium nitidum*
Lp	*Pinus flexilis*
Lpu	*Leptodactylon pungens*
Lpx	*Lupinus* sp.
Ls	*Lotus scoparius*
Lsa	*Lotus salsuginosus*
Lsp	*Lathyrus splendens*
Lsq	*Lepidospartum squamatum*
Lsu	*Lonicera subspicata*
Lt	*Larrea tridentata*
Luca	*Lupinus argenteus heteranthus*
Lul	*Lupinus lepidus lobbii*
Lup	*Lupinus* sp.
Lux	*Lupinus excubitus*
Lx	*Lotus* sp.
Lys	*Stephanomeria spinosa*
M	*Arbutus menziesii*
M2	*Acer macrophyllum*
M3	*Alnus incana tenuifolia*
Ma	*Carpobrotus chilensis*
Mad	*Ericameria discoidea*
Marsh	Marsh
Mas	*Ericameria suffruticosa*
Mbu2	*Melica bulbosa*
Mc	*Myrica californica*
Md	Meadow
Md2	Meadow
Mdw	Meadow
Mh	*Myrica hartwegii*
Mhi	*Medicago polymorpha*
Mic	*Micropus californicus*
Mill	Mill
Ml	*Mirabilis californica*
Mm	*Mimulus moschatus*
Mo	*Monardella odoratissima*
Moss	Moss
Mp	*Pinus radiata*
Mpa	*Malva parviflora*
Mpe	*Claytonia perfoliata*
Mv	*Marrubium vulgare*
Mya	*Cupressus abramsiana*
My	*Cupressus macrocarpa*
Mz	*Manzanita* sp.
N	*Torreya californica*
N2	*Acer negundo californicum*
Nav2	*Navarretia* sp.
Ng	*Nicotiana glauca*
Np	*Turricula parryi*
Npa	*Nolina parryi*
Ny	*Cupressus macnabiana*
O	*Cupressus lawsoniana*
O3	*Fraxinus latifolia*
Ob	*Opuntia bigelovii*
Oc	*Oemleria cerasiformis*

Species code	Species and land cover name used
Ok	*Quercus kelloggii*
Olive	Olive orchard
Oo	*Opuntia X occidentalis*
Ool	*Opuntia littoralis*
Ot	*Opuntia treleasei*
Ox	*Opuntia* sp.
P	*Pinus monophylla*
P3	*Washingtonia filifera*
Pa	*Heteromeles arbutifolia*
Pad	*Prunus andersonii*
Pal	*Palafoxia arida*
Pan	*Keckiella antirrhinoides*
Pb	*Keckiella breviflora*
Pba	*Phacelia brachyloba*
Pbc	*Ptelea crenulata*
Pbs	*Polygonum bistortoides*
Pc	*Keckiella cordifolia*
Pci	*Plectritis ciliosa*
Pcm	*Penstemon* sp.
Pct	*Horkelia tridentata tridentata*
Pd	*Prunus virginiana demissa*
Pda	*Polygonum davisiae*
Pe	*Prunus emarginata*
Pf	*Prunus fasciculata*
Pfr	*Prunus fremontii*
Pg	*Purshia tridentata glandulosa*
Phb	*Phyllodoce breweri*
Phd	*Phlox cespitosa*
Phh	*Phacelia heterophylla virgata*
Pht	*Phacelia thermalis*
Pi	*Prunus ilicifolia*
Pj	*Prosopis glandulosa torreyana*
Pl	*Philadelphus lewisii*
Plb	*Horkelia cuneata puberula*
Pln	*Plagiobothrys nothofulvus*
Pm	*Pickeringia montana*
Po	*Pellaea mucronata*
Pos	*Ivesia santolinoides*
Pot	*Populus tremuloides*
Pp	*Pinus quadrifolia*
Ppo	*Psorothamnus polydenius*
Ps	*Penstemon spectabilis*
Ps2	*Poa secunda secunda*
Psc2	*Poa secunda secunda*
Pse	*Pluchea sericea*
Psp2	*Poa secunda secunda*
Psu	*Prunus subcordata*
Pt	*Purshia tridentata*
Pta	*Pteridium aquilinum pubescens*
Pur	*Arctostaphylos purissima*
Px2	*Poa* sp.
Q	*Chrysolepis chrysophylla*
Qa	*Quercus agrifolia agrifolia*
Qc	*Quercus chrysolepis nana*
Qd	*Quercus berberidifolia*
Qdo	*Quercus douglasii*
Qdu	*Quercus durata*
Qe	*Quercus engelmannii*
Qg	*Quercus garryana*
Qgb	*Quercus garryana*
Qgs	*Quercus garryana*
Qk	*Quercus kelloggii*
Qp	*Quercus palmeri*

Species code	Species and land cover name used
Qs	*Quercus sadleriana*
Qv	*Quercus vaccinifolia*
Qw	*Quercus wislizeni frutescens*
R	*Sequoia sempervirens*
R1	*Abies magnifica*
R2	*Alnus rubra*
Ra	*Ribes aureum*
Rb	*Ribes bracteosum*
Rc	*Rhamnus californica*
Rca	*Ribes californicum*
Rce	*Ribes cereum*
Rci	*Rhamnus ilicifolia*
Rcl	*Rosa californica*
Rcr	*Rhamnus crocea*
Rct	*Rhamnus tomentella tomentella*
Rd	*Toxicodendron diversilobum*
Rep	Reproduction
Res	Residence
Rha	*Rhamnus* sp.
Ri	*Rhus integrifolia*
Ris	*Ribes* sp.
River	Water
Rl	*Malosma laurina*
Rm	*Ribes malvaceum*
Ro	*Rhus ovata*
Rock	Rock
Ros	Unknown Code
Rp	*Rubus parviflorus*
Rr	*Ribes roezlii*
Rt	*Rhus trilobata*
Rv	*Rubus ursinus*
Rve	*Ribes velutinum*
Rvg	*Ribes velutinum*
S	*Pinus lambertiana*
S1	*Abies magnifica shastensis*
S3	*Platanus racemosa*
Sa	*Salvia apiana*
Saa	*Salicornia virginica*
Sab	*Sarcobatus vermiculatus*
Sad	*Salvia dorrii*
Sal	*Symphoricarpos albus laevigatus*
Salsp	*Salvia* sp.
Sand	Sand
Sar	*Symphoricarpos rotundifolius*
Sas	*Salicornia subterminalis*
Sav	*Sarcobatus vermiculatus*
Sc	*Lepechinia calycina*
Sca	*Simmondsia chinensis*
Sci	*Scirpus acutus*
Scl	*Salvia clevelandii*
Sco2	*Achnatherum coronatum*
Scr	*Salvia dorrii*
Sd	*Senecio flaccidus douglasii*
Sf	*Malacothamnus fasciculatus*
Sg	*Sambucus mexicana*
Sha	*Shepherdia argentea*
Sia	*Sisymbrium altissimum*
Sih	*Malvella leprosa*
Sil	*Silene lemmonii*
Skt	*Salsola tragus*
Sl	*Salvia leucophylla*
Sli	*Ericameria linearifolia*
Sm	*Salvia mellifera*

Species code	Species and land cover name used
Smo	*Symphoricarpos mollis*
So	*Styrax officinalis redivivus*
Sol	*Sonchus oleraceus*
Sos	*Sorbus scopulina*
Sp2	*Nassella pulchra*
Sr	*Sambucus racemosa*
Ss	*Salvia spathacea*
Ss2	*Achnatherum speciosum*
Sso	*Salvia sonomensis*
Stn	*Stellaria nitens*
Str	*Stephanomeria pauciflora*
Su	*Solanum umbelliferum*
Sum	*Suaeda moquinii*
Sv	*Sambucus mexicana*
Sx	*Salix* sp.
Sy	*Cupressus sargentii*
T	*Lithocarpus densiflorus*
Tar2	*Taraxacum* sp.
Tc	*Tetradymia canescens*
Te	*Trientalis latifolia*
Teg	*Tetradymia glabrata*
Tet	*Tetradymia* sp.
Ti	*Trichostema lanatum*
Tla	*Trichostema lanceolatum*
Tm2	Unknown Code
Tp	*Pinus torreyana*
Tri2	*Trifolium variegatum*
Ts	*Tetradymia* sp.
Tule	Tule
Ty	*Cupressus forbesii*
Tyl	*Typha latifolia*
Uc	*Umbellularia californica*
Ue	*Ulex europaeus*
V	*Quercus lobata*
V3	*Fraxinus velutina*
Vc	*Vitis californica*
Vec	*Veratrum californicum californicum*
Vg	*Vitis girdiana*
Vl	*Viguiera laciniata*
Vo	*Vaccinium ovatum*
W	*Quercus wislizeni*
W'	*Pinus monticola*
W1	*Abies concolor*
Wash	Wash
Wat	Water
Water	Water
Resr	Reservoir
Wc	*Juglans californica*
WildH	Wild hay
Wm	*Wyethia mollis*
Wmo	*Wyethia mollis*
Wp	*Pinus albicaulis*
Ws	*Picea breweriana*
Xa	*Salix lasiolepis*
Xcr	*Salix* sp.
Xe	*Salix exigua*
Xr	*Salix laevigata*
Xt	*Xerophyllum tenax*
Y	*Pinus ponderosa*
Yb	*Yucca brevifolia*
Ym	*Yucca schidigera*
Yw	*Yucca whipplei*
#2	desert composite

APPENDIX 4. CONTINUED

Species code	Species and land cover name used
(A)	(*Quercus agrifolia*)
(Atr)	(*Artemisia tridentata*)
(Cb)	(*Cercocarpus betuloides*)
(Cd)	(*Ceanothus leucodermis*)
(Chr)	(*Chrysothamnus* sp.)
(Cnc)	(*Chrysothamnus nauseosus consimilis*)
(Cu)	(Cultivated)
(D')	(*Quercus douglasii*)
(Dp)	(*Pinus sabiniana*)
(Ef)	(*Eriogonum fasciculatum*)
(Gr)	(Grass sp.)
(I)	(*Calocedrus decurrens*)
(J)	(*Pinus jeffreyi*)
(Jc)	(*Juniperus californica*)
(Jo)	(*Juniperus occidentalis*)
(L)	(*Pinus contorta murrayana*)
(Ps2)	(*Poa secunda secunda*)
(Qc)	(*Quercus chrysolepis nana*)
(Qd)	(*Quercus berberidifolia*)
(Qdu)	(*Quercus durata*)
(Qw)	(*Quercus wislizeni frutescens*)
(Res)	(Residence)
(W)	(*Quercus wislizeni*)
(W1)	(*Abies concolor*)
(Wp)	(*Pinus albicaulis*)
(Y)	(*Pinus ponderosa*)
(Yw)	(*Yucca whipplei*)

APPENDIX 5. Summary information about the number of polygons and extent of landcover types in the VTM dataset. This table reports the extents by WHR type. If there is no entry in the WHR2 column, this indicates that this type never appears as the lesser landcover type in a mosaic polygon.

WHR type	# Polygons	Area (ha)	Area (km^2)	WHR1 (km^2)	WHR2 (km^2)
Alkali Desert Scrub	183	181,386.72	1813.87	1215.29	598.58
Alpine Dwarf-Scrub	1	11.07	0.11	0.11	
Annual Grassland	26,361	2,493,051.93	24,930.52	16,703.45	8227.07
Aspen	1397	16,621.51	166.22	111.36	54.85
Barren	5084	984,838.82	9848.39	9848.39	
Bigcone Douglas-Fir	2485	40,590.86	405.91	271.96	133.95
Bitterbrush	554	40,665.5	406.65	272.46	134.2
Blue Oak Woodland	7872	575,031.04	5750.31	3852.71	1897.6
Blue Oak-Foothill Pine	6208	584,171.64	5841.72	3913.95	1927.77
Chamise-Redshank Chaparral	24,594	1,482,483.19	14,824.83	9932.64	4892.19
Closed-Cone Pine-Cypress	1775	42,577.3	425.77	285.27	140.51
Coastal Oak Woodland	16,400	413,077.2	4130.77	2767.62	1363.15
Coastal Scrub	20,787	719,598.95	7195.99	4821.31	2374.68
Cropland	10,953	2,287,121.92	22,871.22	15,323.72	7547.5
Desert Riparian	41	13,766.08	137.66	92.23	45.43
Desert Scrub	848	82,198.27	821.98	550.73	271.25
Desert Succulent Scrub	2	88.86	0.89	0.89	
Desert Wash	77	16,065.61	160.66	107.64	53.02
Douglas Fir	3165	463,911.64	46,39.12	3108.21	1530.91
Dryland Grain Crops	3	78.29	0.78	0.78	
Eastside Pine	1043	55,391.95	553.92	371.13	182.79
Eucalyptus	483	8559.26	85.59	57.35	28.25
Evergreen Orchard	1	10.07	0.1	0.1	
Fresh Emergent Wetland	152	7536.81	75.37	50.5	24.87
Glacier	6	83.19	0.83	0.83	
Jeffrey Pine	6824	423,717.62	4237.18	2838.91	1398.27
Joshua Tree	48	4101.13	41.01	41.01	
Juniper	2207	200,936.8	2009.37	1346.28	663.09
Klamath Mixed Conifer	1786	246,565.04	2465.65	2465.65	
Lacustrine	1874	328,093	3280.93	3280.93	
Lodgepole Pine	2858	187,690.68	1876.91	1257.53	619.38
Low Sage	248	13,059.2	130.59	87.5	43.1
Mixed Chaparral	25,067	955,059.69	9550.6	6398.9	3151.7
Montane Chaparral	12,274	379,163.82	3791.64	2540.4	1251.24
Montane Hardwood	18,983	664,821.89	6648.22	4454.31	2193.91
Montane Hardwood-Conifer	1093	45,000.08	450	301.5	148.5
Montane Riparian	1211	25,536.53	255.37	171.09	84.27
Pasture	18	216.42	2.16	1.45	0.71
Perennial Grassland	677	71,471.24	714.71	714.71	
Pinyon-Juniper	2765	427,897.64	4278.98	2866.91	1412.06
Ponderosa Pine	7728	661,092.49	6610.92	4429.32	2181.61
Red Fir	3886	362,675.06	3626.75	2429.92	1196.83
Redwood	1038	71,584.58	715.85	479.62	236.23
Sagebrush	5547	569,785.19	5697.85	3817.56	1880.29
Saline Emergent Wetland	322	60,783.72	607.84	407.25	200.59
Sierran Mixed Conifer	6667	618,111.45	6181.11	4141.35	2039.77
Subalpine Conifer	4140	191,573.34	1915.73	1283.54	632.19
Unknown	4561	168,449.76	1684.5	1684.5	
Urban	389	151,272.98	1512.73	1013.53	499.2
Valley Foothill Riparian	1454	54,608.97	546.09	365.88	180.21
Valley Oak Woodland	1746	80,122.67	801.23	536.82	264.4
Wet Meadow	3985	96,410.32	964.1	645.95	318.15
White Fir	1675	121,434.12	1214.34	813.61	400.73

EVERGREEN AND DECIDUOUS FERNS OF THE COAST REDWOOD FOREST

Emily E. Burns
Save the Redwoods League, 111 Sutter Street, 11th Floor, San Francisco, CA 94104
eburns@savetheredwoods.org

Jarmila Pittermann
Department of Ecology and Evolutionary Biology, University of California,
Santa Cruz, CA 95064

Christopher Rico
DuPont Pioneer, 18369 County Rd 98, Woodland, CA 95695

Abstract

The understory of California's coast redwood forests boasts an abundance of ferns, half of which are drought deciduous. Despite their ecological importance, little is known about the functional differences between deciduous and perennial ferns. This study explored morphological and physiological leaf traits of an assortment of coast redwood forest fern species sampled from the southern, drier extent of the ecosystem, to determine if deciduous species are less drought tolerant than co-occurring evergreen species because of their shorter leaf lifespan. In mid-summer, all ferns were well hydrated with water potentials above −1 MPa. Although the deciduous ferns were more vulnerable to hydraulic dysfunction by embolism, it is likely that all species experienced similarly low degrees of embolism *in situ*, as inferred from mid-day water potential measurements. Despite their similar water relations when water was not limiting, we observed that deciduous ferns had thinner pinnae because they avoid the late summertime drought by shedding their fronds, in contrast to co-occurring evergreen ferns that invest in sclerophyllous leaves that persist for at least two growing seasons. Our study shows that even within the mesic habitat of the forest understory, ferns can exploit a spectrum of functional strategies that allows them to thrive in separate niches, differences that may become more pronounced in water-limiting habitats.

Key Words: embolism, hydraulic conductivity, leaf allometry, pteridophytes, stomatal conductance, water potential, xylem.

Evergreen plants dominate many ecosystems around the world (Axelrod 1966; DeFries et al. 2000) and in California, where the drought season is limited to less than four months (Mooney and Dunn 1970), evergreens comprise more than 75% of the flora in mesic habitats. By continuously retaining leaves, evergreens benefit from an extended growing season relative to deciduous species that shed their leaves for part of the year in response to seasonal water deficit (Chabot and Hicks 1982; Van Buskirk and Edwards 1995). When drought conditions are prolonged however, deciduous plants benefit from reduced respiratory costs and better water conservation in perennial stem and root tissues by eliminating their leaf area (Mooney and Dunn 1970; Chabot and Hicks 1982; Givnish 2002; Westoby et al. 2002). Interestingly, evergreen and deciduous species can retain leaves for varying lengths of time while occupying the same habitat and sharing the same access to water (Wright et al. 2004; Brodribb and Holbrook 2005). Given this variation in life history strategies, can co-occurring deciduous and evergreen plants vary in drought tolerance?

The coast redwood (*Sequoia sempervirens* [D. Don] Endl.) forests of Northern California host abundant populations of deciduous and evergreen ferns, which often grow side-by-side. Specifically, there are 16 species of shallowly rooted, shade-tolerant species with differing leaf retention strategies (Waring and Major 1964; Grillos 1966). These ferns perennially blanket the forest floor, stream banks, and decomposing logs (Lyons et al. 1988). Ferns typically root in the upper soil layer (Limm 2009), and since the coastal California climate is categorized as Mediterranean with wet winters and low-precipitation summers, water may become limiting in this shallow soil stratum. This is especially relevant after the rainy season when moisture declines and summertime air temperatures increase (Ewing et al. 2009). Half of the coast redwood fern species are drought deciduous and yet surprisingly, little is known about how these ferns with short-lived leaves differ physiologically and morphologically from the evergreen species with which they co-occur.

While coast redwood forest ferns all produce new leaves during the wet season (November to April), the timing of leaf shedding varies by species. Evergreen species including *Polystichum munitum* (Kaulf.) C. Presl (Western sword fern), *Woodwardia fimbriata* Sm. (giant chain fern), and *Dryopteris arguta* (Kaulf.) Maxon (wood fern) retain each leaf cohort produced in the spring for more than two years. They maintain multiple leaf cohorts year-
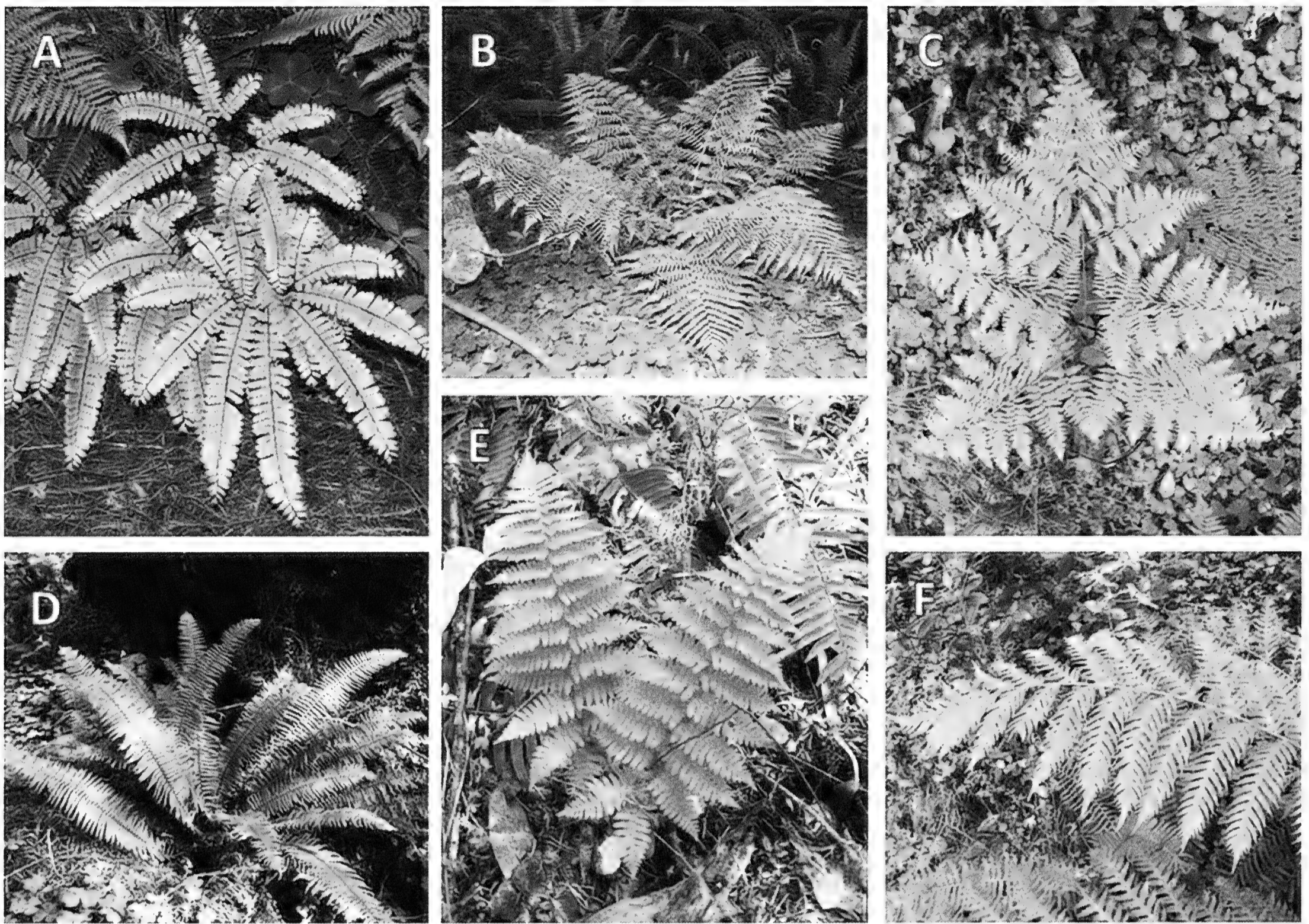
FIG. 1. Diversity of leaf types in ferns studied in southern coast redwood forests range from deciduous, A. *Adiantum aleuticum*, B. *Athyrium filix-femina*, and C. *Pteridium aquilinum*, to evergreen, D. *Polystichum munitum*, E. *Dryopteris arguta*, and F. *Woodwardia fimbriata* for leaves sampled at the Landels-Hill Big Creek Reserve and University of California, Santa Cruz Natural Reserve.

round and only the oldest cohort senesces at the end of each dry season (September to October). In contrast, deciduous species including *Adiantum aleuticum* (Rupr.) C.A. Paris (five-finger fern), *Athyrium filix-femina* (L.) Roth (lady fern), and *Pteridium aquilinum* L. Kuhn (bracken fern) display only one leaf cohort at a time and exhibit crown senescence by the end of each annual dry season. While deciduous ferns ultimately avoid drought through leaf shedding, they do retain leaves through part of the drought season.

This study explored morphological and physiological leaf characteristics of common deciduous and evergreen coast redwood forest ferns to determine if deciduous species exhibit less drought tolerance than co-occurring evergreen species because of their shorter leaf lifespan. Given that evergreen ferns retain foliage year-round regardless of the drought season duration or intensity, it was hypothesized that that long-lived fern leaves would be thicker and have xylem more able to resist hydraulic failure by air entry (cavitation) than shorter-lived leaves that are not constrained by foliar retention throughout the summer.

METHODS

The six most abundant fern species (Fig. 1) in the driest, southern extent of the coast redwood range were compared to test the hypothesis that deciduous ferns exhibit less drought tolerance than evergreen ferns. Measurements were taken mid-summer in the rainless season in order to sample fern baseline physiological responses to declining soil water availability on mature leaf cohorts for all species, but before any drought-induced senescence began in the deciduous species.

Site Descriptions

All ferns were sampled within 50 m of stream edge on alluvial terraces within closed-canopy coast redwood forests (understory PAR = 5–350 μmol) at the southern end of the ecosystem range. Evergreen species *P. munitum* and *W. fimbriata* and deciduous species *P. aquilinum* and *A. aleuticum* were measured at the Landels-Hill Big Creek Reserve (36°4′30.55″N, 121°35′24.73″W) in Monterey County at an elevation of 89 m. Evergreen *D. arguta* and deciduous *A. filix-femina* were measured at the University of California,

Santa Cruz Natural Reserve (36°59′25″N, 122°3′31″W) at an elevation of 179 m. Thirty-year averages from the PRISM Climate Group (2004) show the Landels-Hill study site has similarly moderate air temperature (t_{mean} = 14.7°C; t_{min} = 9.5°C; t_{max} = 20.0°C) to the Santa Cruz site (t_{mean} = 14.5°C; t_{min} = 7.6°C; t_{max} = 21.4°C). In addition, both sites have similar total annual precipitation (Landels-Hill = 765 mm; Santa Cruz = 1121 mm) that falls primarily between October and May and negligible rainfall was measured in July (<1 mm) when the sampling occurred.

Physiology

Physiological variables were measured on ten randomly selected ferns of each species in July 2010 and 2011, a mid-summer month that represents the optimal period when little to no rain falls, soil moisture is declining (Ewing et al. 2009), but before deciduous ferns exhibit physiological decline associated with senescence. Measurements were conducted mid-day, between 1100 and 1300 hr, to assess plant dry-season water stress during the time of day when demand for water was likely greatest. Mid-rachis leaf water potential (ψ_{leaf}) was measured with a Scholander Pressure Chamber (PMS Instruments, Corvallis, OR). Concurrently on the same individuals, leaf stomatal conductance was measured to water vapor (g_s) using a steady state diffusion porometer (Model SC-1, Decagon Devices, Inc., Pullman, WA) calibrated prior to measurements. Species differences were analyzed using Analysis of Variance and Tukey's HSD using JMP software (SAS Institute Inc., San Francisco, CA).

Frond Morphology

Twenty herbivory-free leaves of each species from separate individuals (n = 120) were sampled to represent the full range of mature leaf sizes at each site to determine the allometric relationship between leaf blade length and area. The rachis length of each leaf (stipe excluded) was measured and the combined projected leaf area of the pinnae and rachis (a) was determined digitally using the software ImageJ (Rasband 2007–2012). The software SigmaPlot 12.0 (SYSTAT Software, San Jose, CA) was used to fit a non-linear equation for each species.

The leaf samples were subsequently dried at 60°C for 72 hr and the dry mass of the rachis and pinnae was measured (m, kg). Specific leaf area (SLA) was calculated as

$$SLA = a/m,$$

where a (m^2) is the leaf area as determined by scanning the leaves and measuring area using ImageJ software (Garnier et al. 2001; Rasband 2007–2012). Species differences were analyzed using Analysis of Variance and Tukey's HSD using JMP software (SAS Institute Inc., San Francisco, CA).

Hydraulic Measurements

Hydraulic measurements were conducted on the stipe (petiole) of each fern frond. Stipe segments of 18–20 cm in length were sampled from eight fronds per species from separate individuals that were collected in the field, re-cut underwater to a length of 142 mm, and the ends were shaved smooth with a razor blade. Xylem emboli were removed by degassing submerged stipes overnight under vacuum in distilled water and filtered 20 mM KCl solution (0.22 µm; E-Pure filtration system; Barnstead International, Dubuque, IA). Stipes were mounted on a tubing apparatus and hydraulic conductivity (K) was measured gravimetrically under a pressure of 6–8 kPa using filtered 20 mM KCl solution following the method of Sperry (1993; see also Baer et al., 2016). The average background flow measured (the flow rates observed without a pressure head, both before and after each gravimetric flow measurement) was subtracted from the pressure-induced flow in order to improve accuracy and K was calculated as the flow rate for a given pressure gradient standardized per unit of stipe length. To calculate xylem specific conductivity (K_s), the total xylem area was measured for each stipe by cutting a thin cross-section of the distal end of each stipe segment with a razor blade, staining in phloroglucinol to highlight lignified tissue including xylem, photographing under 100–200× magnification with a digital camera mounted on a Motic BA400 compound microscope (JH Technologies, San Jose, CA), and analyzing the xylem area using ImagePro software (Media Cybernetics, Carlsbad, CA). To calculate leaf-area specific conductivity (K_{leaf}), frond pinnae were scanned and the leaf area was measured using ImageJ software. K_s and K_{leaf} were obtained by dividing K by xylem and leaf area, respectively.

The vulnerability of each species to cavitation in response to a range of xylem pressures was evaluated using the centrifuge method (Pockman et al. 1995; Alder et al. 1997). Stipes were placed securely in a custom rotor designed to fit a Sorvall RC-5C centrifuge (Thermo Fisher Scientific, Waltham, MA) and spun for three min at speeds that induce a known xylem pressure (P_x). Immediately after spinning, K was measured and used to calculate the per cent loss of conductivity (PLC) caused by centrifugation at each P_x, relative to the maximum conductivity after degassing (K_{max}) at P_x = 0 MPa, such that,

$$PLC = 100 \times (1 - K/K_{max}),$$

where K_{max} was determined at P_x = 0 MPa following degassing. The stipe segments were spun progressively to more negative P_x at −0.5 MPa increments until the PLC exceeded 90%, or the most negative P_x achievable by the centrifuge at P_x = −10 MPa, was reached.

Vulnerability curves were measured on eight stipes per species. A Weibull function (Neufeld et al. 1992)
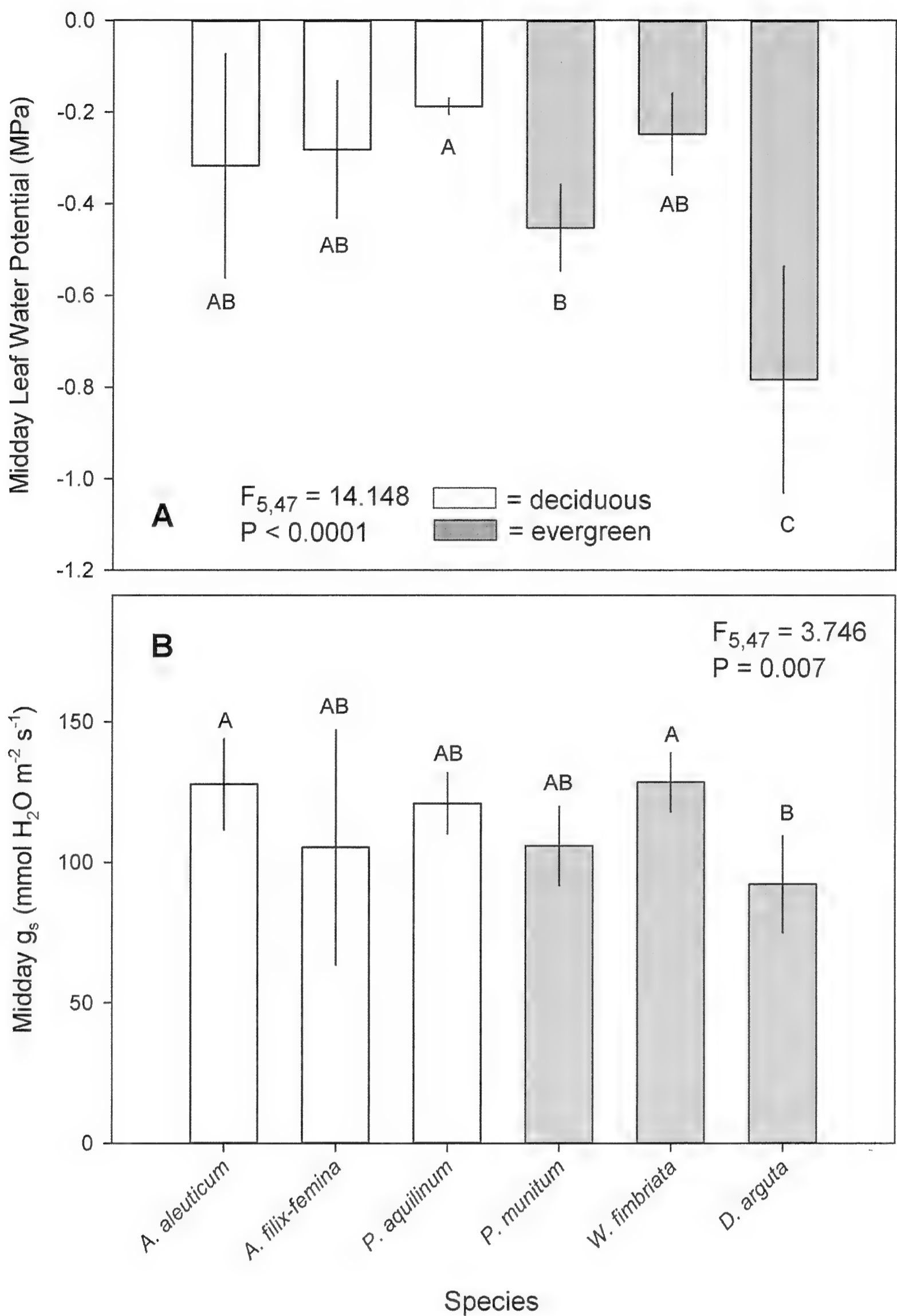
FIG. 2. A. The mean (±SD) midday leaf water potential and B. mean (±SD) midday stomatal conductance (g_s). Measurements were taken in mid-summer at the Landels-Hill Big Creek Reserve (*Adiantum aleuticum*, *Pteridium aquilinum*, *Polystichum munitum*, and *Woodwardia fimbriata*) and University of California, Santa Cruz Natural Reserve (*Athyrium filix-femina*, and *Dryopteris arguta*).

was fit to the pooled vulnerability curve data for each species using statistical software (R Core Team 2016) and the fit was used to calculate the 12%, 50%, and 88% losses of conductivity (P_{12}, P_{50}, P_{88}).

RESULTS

Physiology

Field measures of midday ψ_{leaf} and g_s indicated how hydrated and physiologically active these ferns

were during midsummer (Fig. 2). The observed ψ_{leaf} values at midday indicated all species were well-hydrated. Across taxa, ψ_{leaf} ranged from -0.2 ± 0.01 MPa (mean ± standard deviation) in *Pteridium aquilinum* to -0.8 ± 0.2 MPa in *D. arguta* (Fig. 2A). All ferns exhibited measurable g_s without evidence of mid-day suppression that can occur with low water availability, with values ranging from 92 ± 17 mmol m^{-2} s^{-1} in *D. arguta* to 127.81 ± 16 mmol m^{-2} s^{-1} in *A. aleuticum* (Fig. 2B). While there were statistically significant differences in ψ_{leaf} ($F_{5,47} = 14.148$, p < 0.0001) and g_s ($F_{5,47} = 3.746$, p = 0.007)

DECIDUOUS SPECIES

EVERGREEN SPECIES
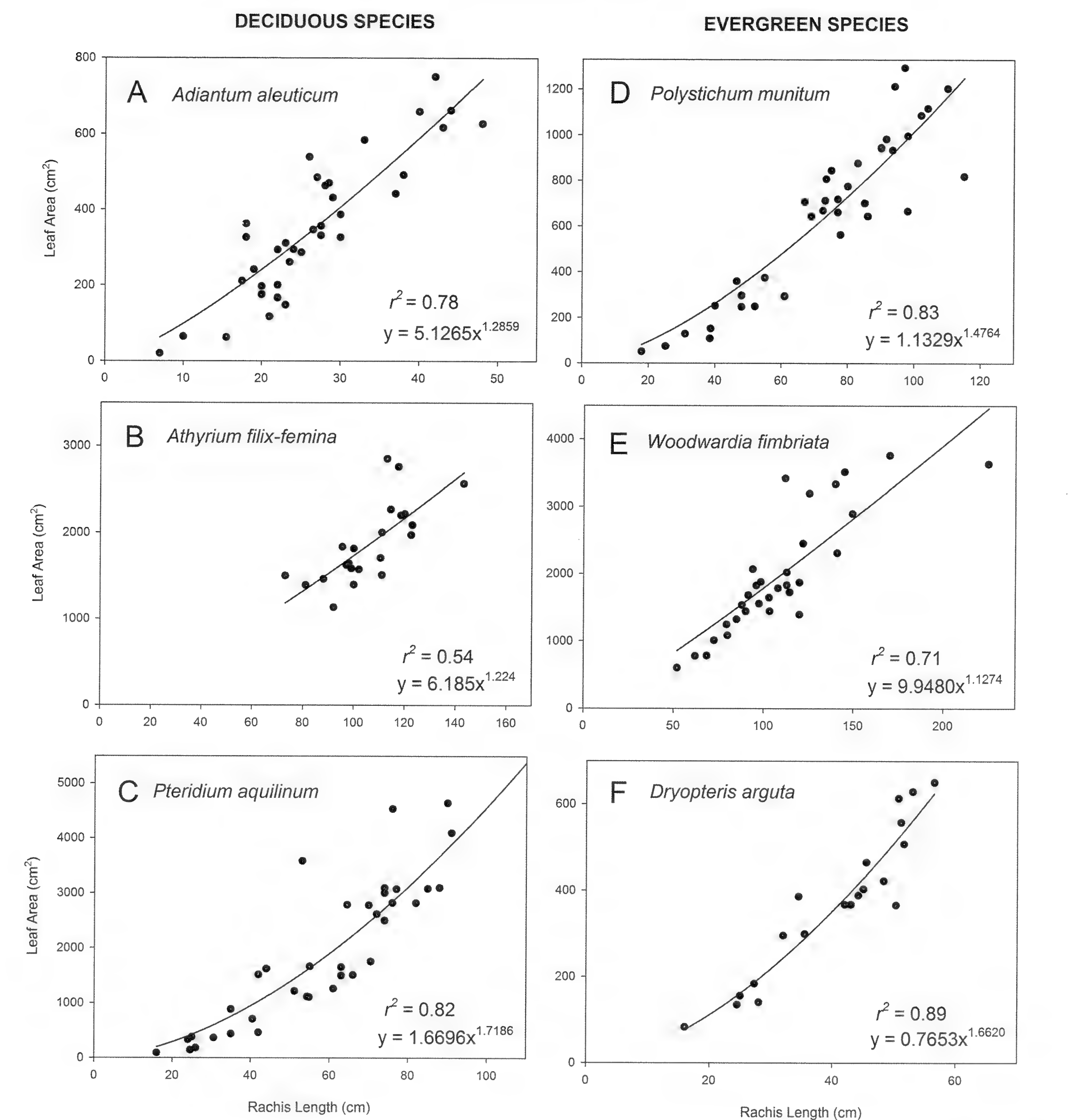
FIG. 3. The nonlinear relationship between leaf area and rachis length for A. *Adiantum aleuticum*, B. *Athyrium filix-femina*, C. *Pteridium aquilinum*, D. *Polystichum munitum*, E. *Woodwardia fimbriata*, and F. *Dryopteris arguta* for leaves sampled at the Landels-Hill Big Creek Reserve and University of California, Santa Cruz Natural Reserve.

between species, deciduous species as a group did not exhibit significantly higher ψ_{leaf} or g_s than evergreen species (Fig. 2).

Frond Morphology

Leaves of all six species exhibited a nonlinear relationship between rachis length and leaf area (Fig. 3A–F) and neither evergreen nor deciduous species had leaves much larger or smaller than the other. In fact, *W. fimbriata* (evergreen) and *P. aquilinum*

(deciduous) had the largest leaves by leaf area and *A. aleuticum* (deciduous) and *D. arguta* (evergreen) had the smallest. SLA varied significantly among species ($F_{5,69} = 31.583$, p < 0.0001), with thinner leaves observed in the three deciduous species, *A. aleuticum*, *A. filix-femina*, and *P. aquilinum* (Fig. 4).

Hydraulic Measurements

While K_s and K_{leaf} varied significantly among species (Fig. 5A, $F_{5,44} = 9.686$, p < 0.0001; Fig. 5B,
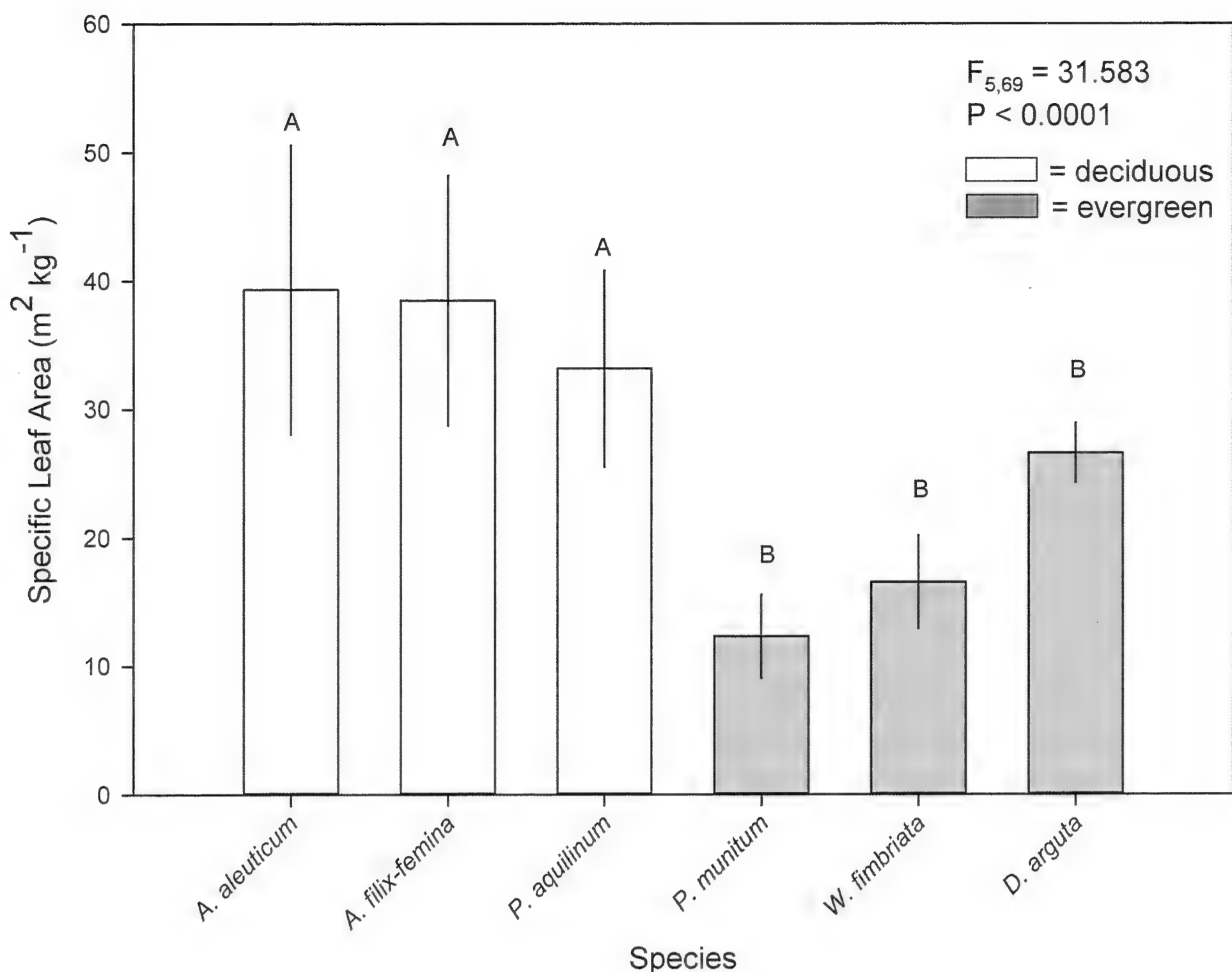
FIG. 4. The mean ($\pm$SD) specific leaf area for deciduous and evergreen species sampled at the Landels-Hill Big Creek Reserve (*Adiantum aleuticum*, *Pteridium aquilinum*, *Polystichum munitum*, and *Woodwardia fimbriata*) and University of California, Santa Cruz Natural Reserve (*Athyrium filix-femina* and *Dryopteris arguta*). Species with the same letter are not significantly different (Tukey's HSD, $\alpha = 0.05$).

$F_{5,36} = 17.77$, $p < 0.0001$), deciduous species as a group did not exhibit higher K_s than evergreen species.

Analyses of the vulnerability curves (Fig. 6) revealed that deciduous species have P_{12} values that ranged from a high vulnerability of -0.2 MPa in *A. filix-femina* to -0.74 MPa in *A. aleuticum*. Evergreen species had P_{12} values from -0.42 MPa in *D. arguta* to -0.93 MPa in *P. munitum*, a similar range as the deciduous species. However, P_{50} values were lower in evergreen species (-5.63 to -7.2 MPa) than deciduous species (-0.74 to -2.81 MPa), indicating that evergreen ferns were more resistant to cavitation at moderate xylem water potential than ferns with shorter leaf lifespans. While deciduous species generally exhibited higher vulnerability to cavitation at low xylem water potentials, the xylem of *A. filix-femina* xylem was exceptionally vulnerable, reaching 100% loss of conductivity by -3.0 MPa. The evergreen ferns were not observed to reach 100% loss of conductivity at the lowest xylem water potential values measured, so the P_{88} values for these species were not reported.

The loss of xylem conductivity was estimated for each species *in situ* using the mid-day leaf water potentials measured in the field during summer, with the assumption that the leaf water potential gradient was minimal in these understory ferns (Fig. 2A). The plants were generally well hydrated and predicted PLC values ranged from 1.9% in *P. aquilinum* to 19.1% in *A. filix-femina*, while the highest PLC was predicted to be 16.5% in *D. arguta*. These low PLC values indicate that ferns maintain a significant buffer against drought-induced embolism since *in situ* PLC values are well below the 50% threshold.

DISCUSSION

The results of this study show that co-occurring evergreen and deciduous fern species share many foliar traits, but differ in leaf mass per area and resistance to drought-induced hydraulic cavitation at low water potentials. During midsummer when soil moisture is declining in the redwood forest (Burgess and Dawson 2004; Ewing et al. 2009), deciduous and evergreen fern species were both well hydrated at mid-day and had similar g_s within the range previously observed in other fern species (Brodribb et al. 2005; Watkins et al. 2010). While negligible rainfall occurred during the weeks before mid-summer physiological measurement, maritime fog may have provided supplemental water (Oberlander 1956; Azevedo and Morgan 1974). These plants
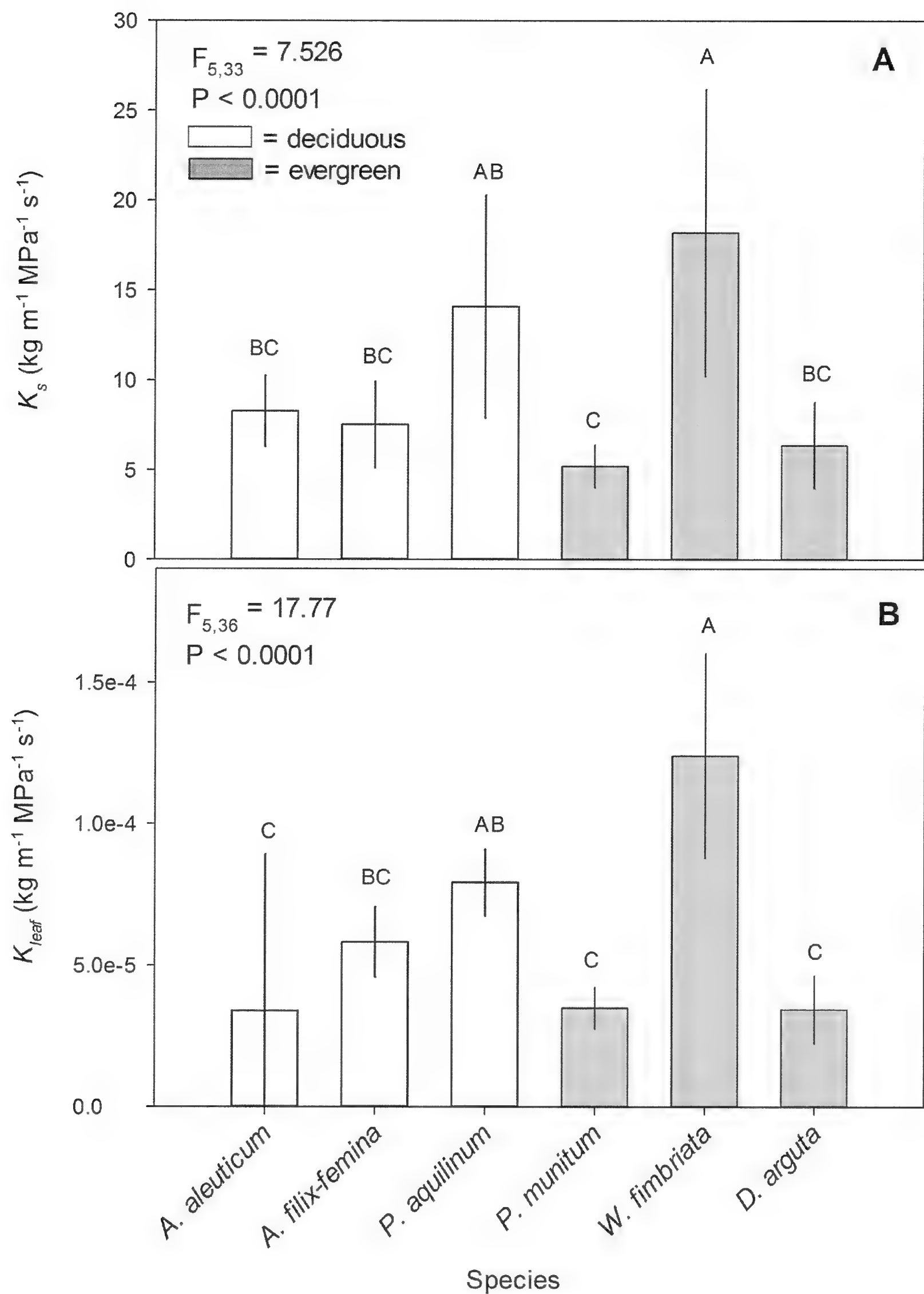
FIG. 5. A. The mean ($\pm$SD) xylem-specific conductivity (K_s) and B. mean ($\pm$SD) leaf-specific conductivity (K_{leaf}) from stipes of deciduous and evergreen species sampled at the Landels-Hill Big Creek Reserve (*Adiantum aleuticum*, *Pteridium aquilinum*, *Polystichum munitum*, and *Woodwardia fimbriata*) and University of California, Santa Cruz Natural Reserve (*Athyrium filix-femina* and *Dryopteris arguta*). Species with the same letter are not significantly different (Tukey's HSD, $\alpha = 0.05$).

would have become measurably less hydrated as the summer progressed, however such drought conditions trigger senescence in deciduous ferns and prevent the species comparisons studied here. In future studies, additional tools such as fluorimetry may be useful for identifying any differences in the earliest signs of drought response between evergreen and deciduous ferns, as was previously shown in north temperate fern species by Reudink et al. (2005).

The vulnerability curves showed that cavitation does in fact differ between evergreen and deciduous ferns. Estimated PLC values at the water potentials

measured mid-day in the field were similar between all species, but the higher P_{50} values measured in the laboratory at milder xylem tensions in the deciduous species indicate that they are more susceptible to cavitation than their evergreen counterparts. This contrast was most striking between the evergreen fern, *W. fimbriata*, and deciduous fern, *A. filix-femina*. These two species commonly co-occur along perennially wet stream banks and yet *W. fimbriata* exhibited $P_{50} = -5.63$ MPa while *A. filix-femina* exhibited $P_{50} = -0.74$ MPa (Fig. 6). Apparent drought tolerance in *W. fimbriata* is consistent with

Deciduous Species   **Evergreen Species**
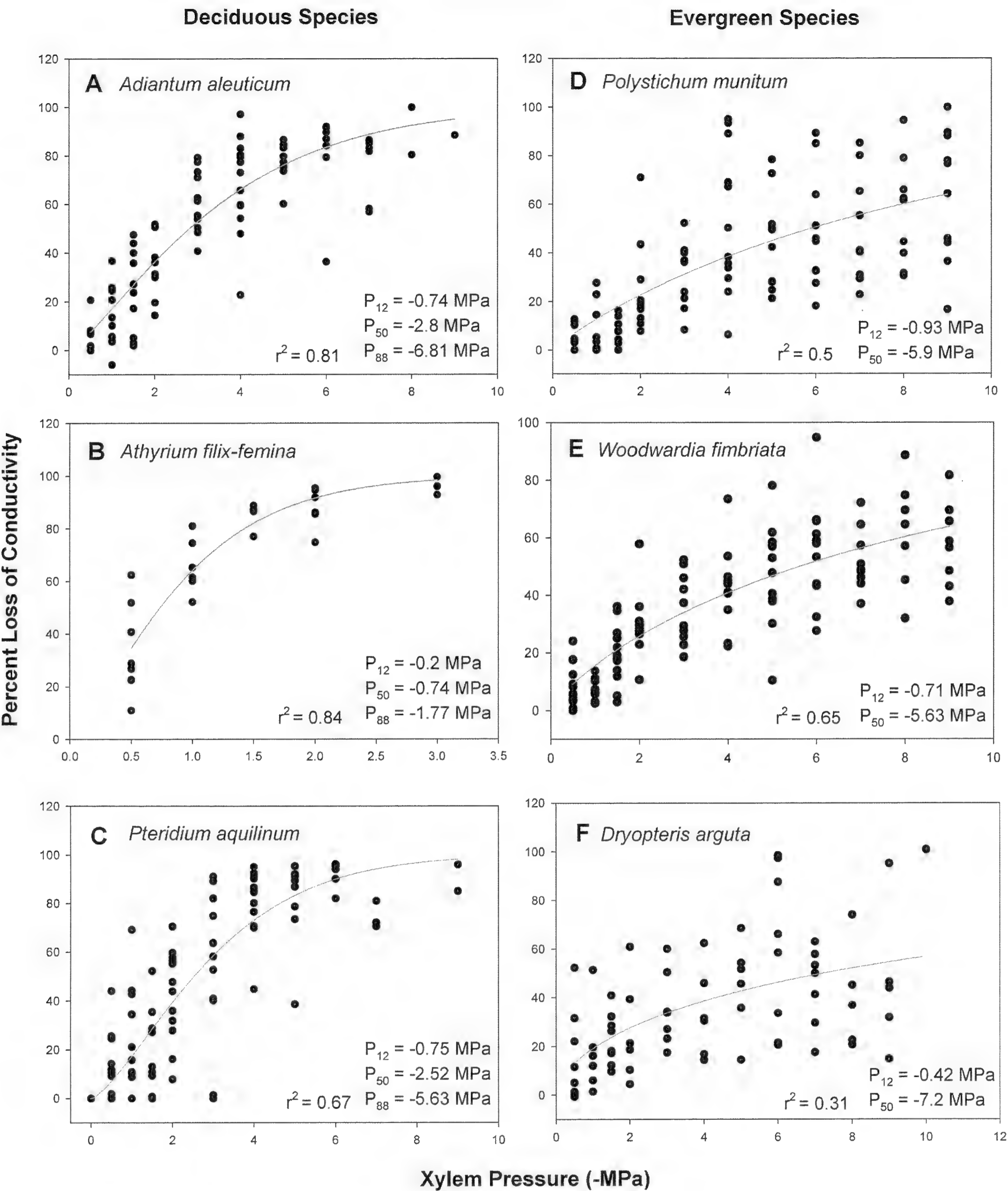
FIG. 6.   The hydraulic response to increasingly negative xylem water potential in the frond stipes of A. *Adiantum aleuticum*, B. *Athyrium filix-femina*, C. *Pteridium aquilinum*, D. *Polystichum munitum*, E. *Woodwardia fimbriata*, and F. *Dryopteris arguta* for leaves sampled at the Landels-Hill Big Creek Reserve and University of California, Santa Cruz Natural Reserve. Vulnerability curves were obtained using the centrifugal method of Alder et al. (1997).

observations that this species can inhabit seasonally dry soils and establish further away from waterways than *A. filix-femina* (Burns and Pittermann personal observations). The higher vulnerability to cavitation in *A. filix-femina* may be a deciduous strategy, in which this species invests less carbon in xylem structure and avoids drought by senescing leaves in

response to dropping water potentials (Brodribb and Holbrook 2004, 2005). While both species are observed to co-occur in the mesic coast redwood forest, differences in their phylogenetic lineages may also explain greater drought tolerance in *W. fimbriata*, a species with sister taxa in the Blechnaceae that occupy more xeric habitats (Smith et al. 2008).

The observed high resistance to cavitation in *W. fimbriata* and other evergreen species suggests that their preference for moist habitats is not likely due to stipe vulnerability to cavitation, and may be related to other traits. Indeed, one would expect the stipe to exhibit a high degree of cavitation resistance because this segment of the frond supplies water to the distal photosynthetic tissue. Previous studies have shown distal portions of the *W. fimbriata* frond to be significantly more sensitive to drought-induced cavitation than the stipe (Brodersen et al. 2012). In woody plants, drought sensitivity may be highest in distal plant parts such as roots and leaves, so similar segmentation may be occurring in ferns (Sperry and Ikeda 1997; Linton et al. 1998; Brodribb and Holbrook 2004). Altogether, this suggests that the stipe portion of *W. fimbriata* and other perennial ferns may have xylem that is more resistant to drought than required for the water potentials this species typically experiences *in situ* (Pittermann et al. 2011). This could be achieved via variable xylem arrangements (Brodersen et al. 2012; Pittermann et al. 2013) and high resistance to air entry into conduits (Brodersen et al. 2014). Despite occurring in generally mesic habitats, cavitation-resistant xylem may still provide an advantage to this species during extreme events such intense or prolonged droughts that would otherwise render the evergreen fern crown susceptible to hydraulic failure. Watkins et al. (2010) found that tropical epiphytic ferns had greater resistance to cavitation than terrestrial fern species which suggests we may find even higher drought tolerance in coast redwood forest ferns if we compare our study species with epiphytic ferns of the redwood forest canopy (e.g., *Polypodium scouleri* Hook. & Grev.; Sillett and Bailey 2003). Further research is needed to investigate greater contrasts between evergreen and deciduous species at more xeric margins of the species' natural range.

Deciduous ferns had significantly higher leaf area per mass than evergreen ferns, a trend commonly observed in among both seed-free and seed-bearing taxa (Merino et al. 1982; Aerts 1995; Givnish 2002; Karst and Lechowicz 2007). This is likely due to the fact that short-lived leaves do not have the same structural requirements needed to withstand biotic and abiotic stress over long periods of time (Chabot and Hicks 1982; Westoby et al. 2002). While carbon to nitrogen ratios and other leaf chemical constituents were not analyzed in this study, other studies suggest that deciduous leaves may be as costly to produce as evergreen species because plants invest more in photosynthetic proteins while investing less in protective structural and defensive chemicals (Merino et al. 1982; Aerts 1985). This variation in leaf allocation strategies may explain in part the absence of differences between evergreen and deciduous ferns with respect to stomatal conductance, a proxy for photosynthesis. Alternatively, there may be little need for dramatically different physiological strategies in a consistently cool and shady understory habitat of the redwood forest.

Given that deciduous ferns were neither larger nor observed losing more water at mid-day (exhibited similar g_s) than evergreen species in mid-summer, ferns with short-lived leaves may simply exhibit different phenological and life-history strategies in mesic habitats. Aerts (1995) suggests that deciduous species with leaves living for 9–10 months share similar foliar traits with leaves that live for 2–3 years. In addition, Sato (1990) found that summer green ferns often resemble evergreen species in the juvenile sporophyte stage. We know little about the recruitment strategies of each species but recruitment phenology may vary between evergreen and deciduous ferns, with seasonally deciduous taxa opportunistically recruiting in early summer, whilst perennial taxa have a broader moisture window. Investigating the drought tolerance of young sporophytes and the gametophyte life stages warrants further research.

In conclusion, co-occurring evergreen and deciduous species of the coast redwood forest exhibit similar physiology and hydraulic efficiency and differ most in leaf thinness and vulnerability to cavitation at low water potentials. It should be noted that this was a conservative study—one where the water was not limiting and future work in more water-limiting habitats or conditions may reveal even greater difference because evergreen and deciduous species. A recent study of seasonal water relations in *P. munitum* and *D. arguta* has shown that prolonged drought stress can induce severe losses of physiological function even in these drought-tolerant species (Baer et al. 2016), suggesting deciduous ferns are likely to be much more vulnerable to severe water deficit. Despite the perennials' ability to passively recover hydraulic conductivity following persistent water stress (Baer et al. 2016), the legacy effects on growth and fitness are poorly understood, and may have profound effects on the composition of the redwood forest understory. If California drought intensifies as temperature climbs in the decades ahead (Hayhoe et al. 2004; Loarie et al. 2009), our results will provide important *in situ* reference physiology data for these species that offer a baseline for comparison with future drought responses.

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JEPSON MANUAL GEOGRAPHIC SUBDIVISION BOUNDARY CHANGES FOR THE KLAMATH AND CASCADE RANGES OF NORTHWESTERN CALIFORNIA AND IMPLICATIONS FOR REGIONAL FLORISTICS

Len Lindstrand III

North State Resources, Inc., 5000 Bechelli Lane, Suite 203, Redding, CA 96002
lindstrand@nsrnet.com

Julie Kierstead Nelson

Shasta-Trinity National Forest, 3644 Avtech Parkway, Redding, CA 96002

David Baxter[1]

University and Jepson Herbaria, 1001 Valley Life Sciences Building, University of California, Berkeley, CA 94720

Abstract

When The Jepson Manual: Higher plants of California was published in 1993, its Geographic Subdivisions of California map included an area of Klamath Ranges geology in its Cascade Ranges subdivision, creating an anomaly with floristic ramifications. We aim to correct that anomaly in this paper. This incorrect designation leads to several issues, including ecologic and geologic inconsistences, and problematic results when conducting floristic analysis in the eastern Klamath Ranges. Botanical field surveys for several recent projects in the eastern Klamath Ranges, newly available digitized data made available online by the Consortium of California Herbaria, and several new taxa recently published from the eastern Klamath Ranges provided means and rationale to make much-needed changes to the Klamath Ranges boundary. Using personal experience, existing ecologic and geologic references, and GIS analysis we revised the Klamath and Cascade Ranges boundaries, provided geographic range updates for over 230 plant taxa, and updated the existing California Geographic Subdivisions descriptions to reflect the boundary revisions. Herein we present the revised map boundary, describe our analysis and results, and provide floristic analysis made possible by the map revisions.

Key Words: Biogeographical range, California Floristic Province, Cascade Ranges, Endemics, Geographic Subdivisions of California, Jepson Flora Project, Jepson Manual, Klamath Ranges.

One of the foundational objectives of providing geographic ranges in a botanical reference is to summarize known occurrence information in a way that allows the user to predict where a particular plant taxon may be expected to occur in nature. Traditionally, most manuals used arbitrary political borders, such as county and state boundaries, to describe geographic range. There are unfortunate consequences of using this approach when the political units used to describe plant distributions are physically and biologically heterogeneous; for instance, a single county in California may include portions of the Coast Ranges, the Central Valley, and the Sierra Nevada. This heterogeneity reduces the predictive power of range descriptions and obfuscates bioregional floristic patterns. When published in 1993, the Jepson Manual: Higher plants of California (TJM) (Hickman 1993) introduced a new system, departing from the common practice of using county boundaries to describe geographic range, by combining natural landscape features such as geology, topography, and vegetation patterns to create geographic units that enhance the effectiveness of geographic data in predicting plant occurrences. The TJM geographic system used a map (Jepson map) influenced by existing well-known sources describing California's floristic patterns (Raven and Axelrod 1978; Küchler 1988) to better portray California's diverse vegetation, resulting from combinations of physical parameters and climate. This system was slightly modified and again used for the second edition of TJM (TJM2) published in 2012 (Baldwin et al. 2012). This system and map is based on a hierarchy beginning with three broadly defined floristic provinces—the California Floristic Province, Great Basin Province, and Desert Province, then 25 subregions, and ending with 35 subdivisions. The Jepson map has become the standard botanical geographic range system for California and has also been widely used as the geographical range standard for other applications (e.g., CalFlora, Consortium of California Herbaria).

Inevitably, geographic range classifications developed for large areas will need periodic revision as new information becomes available, particularly in a biologically and physically diverse state such as California. Even the best classification systems will warrant refinement of areas that have been

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[1] Present address: Faculty of Information, University of Toronto, 140 St. George St., Toronto, ON, Canada M5S 3G6.
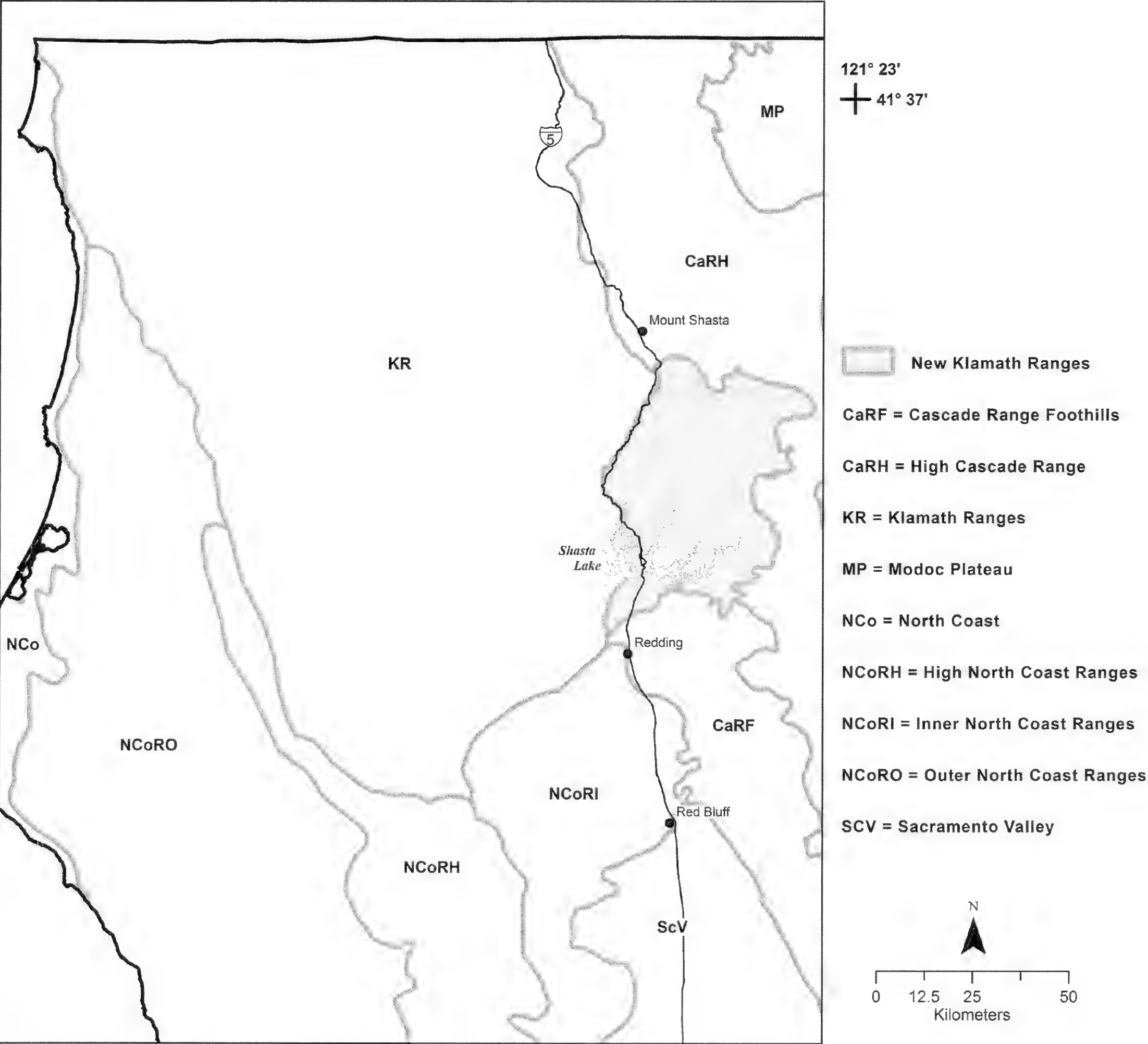
FIG. 1. Portion of the Jepson Map showing the Klamath Ranges, Cascade Ranges, and the new eastern Klamath Range expansion area.

poorly sampled. The Klamath Ranges Subregion (KR), particularly the southeastern Klamath Mountains, represents one such area now deserving refinement. The KR is a geologically old and distinct part of northern California well known for geologic complexity, including many ultramafic substrates and high conifer diversity, with a notable concentration of relict and disjunct conifer species. At its TJM2 eastern boundary the predominantly metamorphic KR meets the volcanic Cascade Ranges (CaR) in an area roughly interpreted by the Jepson map as the Interstate 5 corridor north of Redding, Shasta County, California, to the Oregon border. North of the California-Oregon border, the KR is generally referred to as the Siskiyou Mountains or Siskiyous ecoregion (Meyers et al. 2015).

Unfortunately, this interpretation omits most of the southeastern Klamath Mountains, a significant

portion of the KR that is unique in its own right, placing the area instead into the CaR. This interpretation places large areas of limestone and other metasedimentary geology in the CaR, which is inconsistent with the Baldwin et al. (2012) geographic description of this region as "characterized by volcanics." These issues lead to problematic results when conducting floristic analysis in the KR and CaR. For example, the famous Shasta snow-wreath (*Neviusia cliftonii* Shevock, Ertter & D.W. Taylor), as well as Shasta eupatory (*Ageratina shastensis* [D.W. Taylor & Stebbins] R.M. King & H. Rob., and Shasta County arnica (*Arnica venosa* H.M. Hall), all rare KR endemics, have been described in TJM or TJM2 as either entirely or partially occurring in the CaR because of the misinterpreted KR boundary.

Use of the term "Shasta" in the common names of many eastern KR endemics contributes to the

TABLE 1. List of 141 Jepson manual distribution string changes to 114 plant taxa occurring in the revised Klamath Ranges Boundary. CaR = Cascade Ranges; CaRF = Cascade Range Foothills; CaRH = High Cascade Range; KR = Klamath Ranges; eKR = Eastern Klamath Range.

Taxon	Distribution string change
Acmispon grandiflorus (Benth.) Brouillet var. *macranthus* (Greene) Brouillet	KR added; CaR removed
Aconogonon newberryi (Small) Sojâk	KR added
Adiantum capillus-veneris L.	KR added
Ageratina shastensis (D.W. Taylor & Stebbins) R.M. King & H. Rob.	KR added; CaR removed
Agrostis elliottiana Schult.	KR added
Amorpha californica Nutt. var. *californica*	CaRF removed
Anisocarpus scabridus (Eastw.) B.G. Baldwin	KR added
Anthoxanthum aristatum Boiss. subsp. *aristatum*	KR added; CaRF removed
Anthoxanthum odoratum L.	KR added
Antirrhinum cornutum Benth.	KR added
Antirrhinum vexillocalyculatum Kellogg subsp. *breweri* (A. Gray) D.M. Thomps.	CaRF added; CaRH removed
Aristolochia californica Torr.	CaR made CaRF (CaRH removed)
Arnica venosa H.M. Hall	CaRH removed
Arundo donax L.	KR added
Boechera breweri (S. Watson) Al-Shehbaz subsp. *shastaensis* Windham & Al-Shehbaz	CaR made CaRF (CaRH removed)
Brasenia schreberi J.F. Gmel.	KR added
Brodiaea californica Lindl.	KR added
Brodiaea rosea (Greene) Baker	KR added
Cacaliopsis nardosmia (A. Gray) A. Gray	CaRH removed
Calochortus syntrophus Callahan	KR added
Cardamine pachystigma (S. Watson) Rollins	KR added; CaR removed
Carduus pycnocephalus L. subsp. *pycnocephalus*	KR added
Castilleja affinis Hook. & Arn. subsp. *affinis*	KR added
Ceanothus lemmonii Parry	CaRH added
Ceanothus oliganthus Nutt. var. *sorediatus* (Hook. & Arn.) Hoover	KR added
Centromadia fitchii (A. Gray) Greene	eKR added
Chaenactis suffrutescens A. Gray	CaRH removed
Cheilanthes cooperae D.C. Eaton (*Myriopteris cooperae* ([D.C. Eaton] Grusz & Windham*)*	KR added; CaR removed
Chondrilla juncea L.	KR added
Cicuta douglasii (DC.) J.M. Coult. & Rose	KR added
Clarkia borealis E. Small subsp. *arida* E. Small	eKR added
Crucianella angustifolia L.	KR added; CaRH added
Crypsis schoenoides (L.) Lam.	KR added
Cyperus niger Ruiz & Pav.	KR added; CaRH added
Cypripedium fasciculatum Kellogg ex S. Watson	CaR removed
Delphinium gracilentum Greene	KR added; CaR added
Delphinium variegatum Torr. & A. Gray subsp. *variegatum*	eKR added
Distichlis spicata (L.) Greene	KR added; CaR added
Dittrichia graveolens (L.) Greuter	KR added; CaRF added
Echinochloa colona (L.) Link	eKR added; CaR removed
Eriogonum congdonii (S. Stokes) Reveal	CaRH removed
Eriogonum umbellatum Torr. var. *modocense* (Greene) S. Stokes	KR added
Eriogonum umbellatum Torr. var. *polyanthum* (Benth.) M.E. Jones	KR added
Eriogonum ursinum S. Watson var. *ursinum*	KR added
Eriogonum wrightii Torr. ex Benth. var. *trachygonum* (Torr. ex Benth.) Jeps.	CaR removed
Eriophorum crinigerum (A. Gray) Beetle (*Calliscirpus criniger* [A. Gray] C.N. Gilmour, J.R. Starr & Naczi)	CaR removed
Eriophorum gracile W.D.J. Koch ex Roth	KR added
Erythronium californicum Purdy	CaRH removed
Erythronium multiscapoideum (Kellogg) A. Nelson & P.B. Kenn.	KR added; CaRH added
Eurybia integrifolia (Nutt.) G.L. Nesom	KR added
Festuca trachyphylla (Hack.) Krajina	KR added; CaR added
Fraxinus dipetala Hook. & Arn.	KR added; CaRH added
Fritillaria affinis (Schult. & Schult. f.) Sealy	CaRH removed
Fritillaria eastwoodiae R.M. Macfarlane	KR added
Galium sparsiflorum W. Wight subsp. *glabrius* Dempster & Stebbins	KR added
Genista monspessulana (L.) L.A.S. Johnson	KR added; CaRH added
Glyceria declinata Bréb.	KR added
Grindelia camporum Greene	KR added

TABLE 1. CONTINUED

Taxon	Distribution string change
Heterotheca oregona (Nutt.) Shinners var. *oregona*	CaR removed
Heterotheca oregona (Nutt.) Shinners var. *rudis* (Greene) Semple	CaR removed
Horkelia tridentata Torr. var. *tridentata*	eKR added
Keckiella breviflora (Lindl.) Straw var. *glabrisepala* (D.D. Keck) N.H. Holmgren	CaR added
Lepidium heterophyllum (S. Watson) M.E. Jones	KR added
Lewisia cantelovii J.T. Howell	CaRH removed
Lewisia cotyledon (S. Watson) B.L. Rob. var. *cotyledon*	CaRH removed
Lewisia cotyledon (S. Watson) B.L. Rob. var. *howellii (S. Watson) Jeps.*	CaRH removed
Lilium washingtonianum Kellogg subsp. *washingtonianum*	KR added
Limnanthes alba Hartw. ex Benth. subsp. *versicolor* (Greene) C.T. Mason	KR added
Lithophragma bolanderi A. Gray	KR added
Logfia gallica (L.) Coss. & Germ.	KR added
Lomatium bicolor (S. Watson) J.M. Coult. & Rose var. *leptocarpum* (Torr. & A. Gray) Schlessman	KR added
Lomatium caruifolium (Hook. & Arn.) J.M. Coult. & Rose var. *denticulatum* Jeps.	KR added
Lomatium marginatum (Benth.) J.M. Coult. & Rose var. *marginatum*	CaRH removed
Lonicera involucrata (Richardson) Banks ex Spreng. var. *involucrata*	KR added; CaRH added
Luina hypoleuca Benth.	CaRH removed
Lupinus albifrons Benth. var. *albifrons*	KR added
Lupinus lepidus Douglas ex Lindl. var. *lobbii* (S. Watson) C.L. Hitchc.	KR added; CaRH added
Lychnis coronaria (L.) Desr.	KR added
Marah watsonii (Cogn.) Greene	KR added; CaRH added
Mimulus bolanderi A. Gray	KR added
Monardella breweri A. Gray subsp. *lanceolata* (A. Gray) A.C. Sanders & Elvin	KR added
Monardella odoratissima Benth. subsp. *glauca* (Greene) Epling	KR added
Monardella sheltonii Torr.	KR added
Nemacladus capillaris Greene	KR added; CaRF added
Panicum dichotomiflorum Michx. subsp. *dichotomiflorum*	eKR added; CaRH added
Panicum oligosanthes Schult. var. *scribnerianum* (Nash) Fernald	CaR removed
Parnassia cirrata Piper var. *intermedia* (Rydb.) P.K.Holmgren & N.H. Holmgren	CaRH removed
Pellaea mucronata (*D.C. Eaton*) *D.C. Eaton* var. *mucronata*	KR added
Penstemon azureus Benth. var. *angustissimus* A. Gray	KR added
Penstemon filiformis (D.D. Keck) D.D. Keck	eKR to KR
Penstemon newberryi A. Gray var. *newberryi*	KR added
Penstemon rydbergii A. Nelson var. *oreocharis* (Greene) N.H. Holmgren	KR added
Petrorhagia dubia (Raf.) G. López & Romo	KR added
Poa palustris L.	KR added
Polygonum majus (Meisn.) Piper	KR added
Polystichum munitum (Kaulf.) C. Presl	CaR removed
Potamogeton crispus L.	KR added; CaR added
Ptelea crenulata Greene	eKR added; CaRH added
Quercus douglasii Hook. & Arn.	KR added
Quercus lobata Née	KR added
Quercus wislizeni A. DC. var. *wislizeni*	KR added
Sanicula tuberosa Torr.	KR added
Silene campanulata S. Watson subsp. *glandulosa* C.L. Hitchc. & Maguire	CaR removed
Sparganium natans L.	eKR added
Staphylea bolanderi A. Gray	eKR added
Streptanthus longisiliquus G.L. Clifton & R.E. Buck	eKR added
Symphyotrichum bracteolatum (Nutt.) G.L. Nesom	KR added
Symphyotrichum frondosum (Nutt.) G.L. Nesom	KR added
Tauschia kelloggii (A. Gray) J.F. Macbr.	KR added
Thermopsis gracilis Howell	CaR removed
Trifolium ciliolatum Benth.	KR added
Trillium chloropetalum (Torr.) Howell	KR added
Vaccinium parvifolium Sm.	CaRH removed
Wyethia glabra A. Gray	KR added

TABLE 2. Summary of 141 Jepson manual distribution string changes, classification, and life form for 114 plant taxa occurring in the revised Klamath Ranges Boundary. CaR = Cascade Ranges; CaRF = Cascade Range Foothills; CaRH = High Cascade Range; KR = Klamath Ranges; eKR = Eastern Klamath Range.

Number of	CaR/CaRF/ CaRH added	CaR/CaRF/ CaRH removed	CaR made CaRF	KR added	eKR added	eKR made KR
Taxa	21	32	2	75	10	1
Families	17	16	2	27	9	1
Genera	21	29	2	61	10	1
Grasses/Herbs	16	25	1	64	8	1
Ferns	0	2	0	2	0	0
Vines	1	1	1	1	0	0
Shrubs	4	4	0	5	2	0
Trees	0	0	0	3	0	0

confusion, since most people naturally associate "Shasta" with Mt. Shasta, the prominent volcanic peak in the southern Cascade Ranges. Instead, "Shasta" in reference to eastern KR flora pertains to the geographic location of the eastern KR as almost entirely in western Shasta County and proximal to Shasta Lake, the large reservoir formed by Shasta Dam, which captures the waters of the upper Sacramento, McCloud, and Pit River watersheds.

Several recent events created an opportunity to revisit eastern KR and CaR boundary issues: botanical field surveys associated with environmental impact analyses for several large public land proposals produced an abundance of new plant distribution and ecological data, digitized Consortium of California Herbaria (CCH) records with coordinates now make floristic analysis and quality control of location data much easier, and several new eastern KR endemic taxa have been recently described (Nesom 2013; Huiet et al. 2015; Nelson and Lindstrand 2015; York et al. 2015). The timing seemed appropriate to make long overdue changes to the KR/CaR boundary.

METHODS

Revising the KR boundary required several steps: (1) determine the geographic area where the new boundary occurs, (2) revise the Jepson map to reflect the updated KR and CaR boundaries, (3) update the existing Jepson map geographic subdivision and subregion descriptions for the KR and CaR to reflect the revised boundaries, (4) determine if plant taxa recorded in this area require geographic range updates to their TJM2 distribution string based on the revised boundaries, and (5) make appropriate geographic range updates to those taxa in the Jepson eFlora (Jepson Flora Project 2014).

We determined the area requiring boundary revisions based on our collective experience in the area and existing geology and ecological subregion maps (Irvin 1994; Miles and Goudy 1997). Once identified, a GIS shapefile of the eastern KR adjustment area was created. A list of taxa whose distribution statements would be affected by this

change (i.e., taxa whose bioregion statement in the Jepson eFlora contained one or two of KR, CaRH, and CaRF, but not all three) was extracted from the Jepson eFlora, and all georeferenced records of those taxa were extracted from the CCH (2014). Using the QGIS software package (Quantum GIS Development Team 2015), we compared specimen points to bioregion polygons. Any taxon with at least one specimen occurrence in the revised KR boundary would require review. In order to best represent the full ranges of plant taxa, all CCH specimen records were resolved to currently accepted nomenclature according to Jepson eFlora synonymy prior to GIS analysis.

The resulting list of plant taxa was reviewed to determine whether: they occur only within the revised KR boundary polygon and require an update to their distribution string to either remove CaR and add KR; retain CaR and add KR; or retain only the CaR designation depending on their occurrence within and out of the revised boundaries. Taxa limited to the revised KR boundary polygon were given the additional designation of "eKR" to represent their eastern KR distribution. Finally, we made revisions to the geographic subdivision and subregion descriptions by developing narrative text describing the new boundaries based on their new geographic locations, emphasizing the underlying geology that unifies the Cascade Ranges and separates it from the Klamath Ranges.

RESULTS

The revised KR boundary encompasses approximately 232,552 hectares and overlaps portions of the (former) CaR, High Cascade Ranges (CaRH), and Cascade Range Foothills (CaRF) subregions (Fig. 1). Approximately 195,544 hectares of the CaRH and 37,008 hectares of the CaRF subregions are now included in the KR. Two-hundred thirty-two plant taxa with only KR or CaRH/CaRF range descriptions occurred in the revised KR boundary, requiring review of their TJM2 and Jepson eFlora distribution string. This review resulted in 141 range description changes for 114 taxa, including 29 taxa previously incorrectly assigned as CaR, CaRH, or CaRF now

TABLE 3. List of plant taxa reaching their California northern distribution in the revised Klamath Ranges Boundary.

Taxon
Acmispon grandiflorus (Benth.) Brouillet var. *macranthus* (Greene) Brouillet
Adiantum shastense Huiet & A.R. Sm.
Ageratina shastensis (D.W. Taylor & Stebbins) R.M. King & H. Rob.
Anisocarpus scabridus (Eastw.) B.G. Baldwin
Aristolochia californica Torr.
Astragalus pauperculus Greene
Brodiaea californica Lindl.
Brodiaea matsonii R.E. Preston
Calochortus monophyllus (Lindl.) Lem.
Calochortus syntrophus Callahan
Calycanthus occidentalis Hook. & Arn.
Calystegia atriplicifolia Hallier f. subsp. *buttensis* Brummitt
Cephalanthus occidentalis L.
Cirsium occidentale (Nutt.) Jeps. var. *venustum* (Greene) Jeps.
Clarkia amoena (Lehm.) A. Nelson & J.F. Macbr. subsp. *whitneyi* (A. Gray) F.H. Lewis & M.E. Lewis
Clarkia borealis E. Small subsp. *arida* E. Small
Clarkia borealis E. Small subsp. *borealis*
Collinsia tinctoria Hartw. ex Benth.
Cordylanthus pilosus A. Gray subsp. *hansenii* (Ferris) T.I. Chuang & Heckard
Datura wrightii Regel
Delphinium gracilentum Greene
Dendromecon rigida Benth.
Eriophyllum lanatum (Pursh) J. Forbes var. *obovatum* (Greene) H.M. Hall
Erythranthe taylorii G.L. Nesom
Erythronium shastense D.A. York, J.K. Nelson & D.W. Taylor
Fritillaria eastwoodiae R.M. Macfarlane
Galium sparsiflorum W. Wight subsp. *glabrius* Dempster & Stebbins
Hesperevax acaulis (Kellogg) Greene var. *robustior* Morefield
Hoita macrostachya (DC.) Rydb.
Hoita orbicularis (Lindl.) Rydb.
Hosackia stipularis Benth. var. *ottleyi* (Isely) Brouillet
Hosackia stipularis Benth. var. *stipularis*
Hypericum concinnum Benth.
Hypericum mutilum L.
Keckiella breviflora (Lindl.) Straw var. *glabrisepala* (D.D. Keck) N.H. Holmgren
Leptosiphon latisectus (E.G. Buxton) J.M. Porter & L.A. Johnson
Lewisia cantelovii J.T. Howell
Limnanthes alba Hartw. ex Benth. subsp. *alba*
Lomatium caruifolium (Hook. & Arn.) J.M. Coult. & Rose var. *denticulatum* Jeps.
Lomatium marginatum (Benth.) J.M. Coult. & Rose var. *marginatum*
Marah watsonii (Cogn.) Greene
Mimulus bolanderi A. Gray
Monardella breweri A. Gray subsp. *lanceolata* (A. Gray) A.C. Sanders & Elvin
Myriopteris cooperae (D.C. Eaton) Grusz & Windham
Neviusia cliftonii Shevock, Ertter & D.W. Taylor
Odontostomum hartwegii Torr.
Pellaea andromedifolia (Kaulf.) Fée
Penstemon azureus Benth. var. *angustissimus* A. Gray
Phacelia vallicola Congdon ex Brand
Plagiobothrys glyptocarpus (Piper) I.M. Johnst. var. *glyptocarpus*
Ptelea baldwinii Torr. & A. Gray subsp. *crenulata* (Greene) A.E. Murray
Ranunculus canus Benth.
Sedella pumila (Benth.) Britton & Rose
Sedum obtusatum A. Gray subsp. *paradisum* Denton
Selaginella hansenii Hieron.
Sidalcea gigantea G.L. Clifton, R.E. Buck & S.R. Hill
Staphylea bolanderi A. Gray
Streptanthus longisiliquus G.L. Clifton & R.E. Buck
Styrax redivivus (Torr.) L.C. Wheeler
Torreya californica Torr.
Vaccinium shastense J.K. Nelson & Lindstrand subsp. *shastense*
Wyethia glabra A. Gray
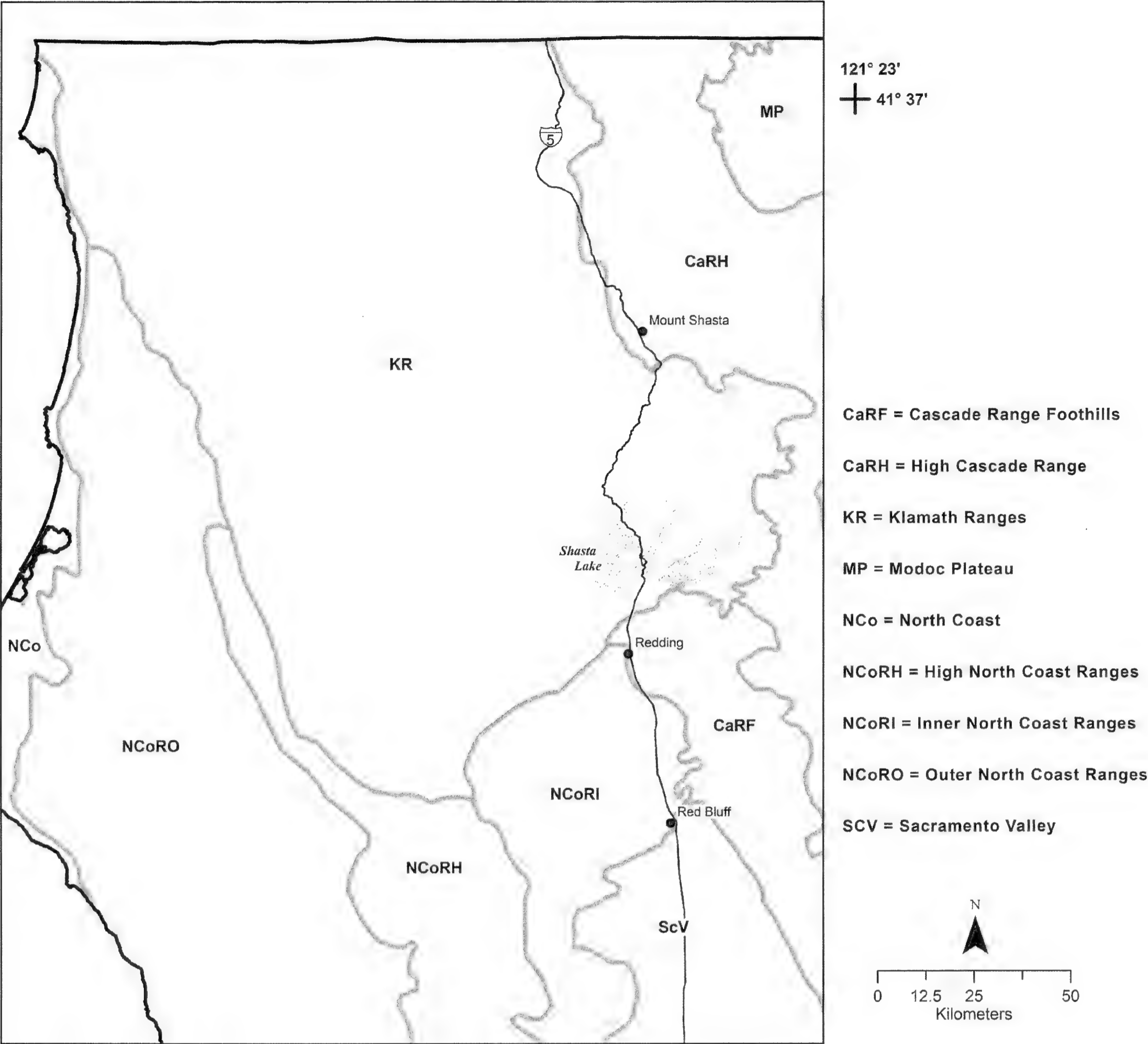
FIG. 2. Revised Klamath Ranges and Cascade Ranges Jepson Map boundaries.

included in KR (Table 1). Eighty-five additional taxa also received some type of range description revision (Table 1), while 118 taxa required no revisions. The 114 taxa subject to distribution string changes overall included 92 genera in 38 families, and consisted of 93 grass/herb, 13 shrub, three fern, two vine, and three tree species. Most changes resulted from the addition of KR to the distribution string of 75 taxa (Table 2).

The geographic range revisions made possible by the new KR boundary and review of CCH records for plant taxa included in the new KR boundary show 62 native plant taxa reach their California northern extent in the eastern KR (Table 3). Analysis of the geographic range revisions and recent species descriptions (Nesom 2013; Huiet et al. 2015; York et al. 2015) also show six taxa are endemic to the eastern KR, including *Ageratina shastensis, Brodiaea matsonii* R.E. Preston, *Clarkia borealis* E. Small subsp. *arida* E. Small, *Neviusia cliftonii, Erythranthe taylorii* Nesom, and *Erythronium shastense* York et

al. Three taxa, *Adiantum shastense* Huiet et al., *Arnica venosa*, and *Clarkia borealis* E. small subsp. *borealis* are near endemics to the eastern KR, as the majority of their distribution occurs in the eastern KR. Additionally, portions of the restricted distribution of KR endemic *Vaccinium shastense* Nelson & Lindstrand subsp. *shastense* occur in the eastern KR (Nelson and Lindstrand 2015).

The new KR boundary (Fig. 2) now encompasses most of the lands east of Interstate 5, south of Highway 89, and north of Highway 299E to include Shasta Lake, the McCloud and Hosselkus limestone formations, and Grizzly Peak, the highest point in the eastern KR at 1905 m (6250 ft) elevation, on the divide between the Pit and McCloud River watersheds. The southern portion of the KR now combines with the northern portions of the Inner North Coast Ranges and Cascade Range Foothills to form a contiguous horseshoe-shaped band of similar vegetation around the head of the Sacramento Valley

(Fig. 2). The new CaR boundary now starts entirely east and south of Shasta Lake and abuts the Inner North Coast Ranges subregion along Interstate 5 from west of Redding south to Red Bluff (Fig. 2).

The new KR boundary, updated CaRH and CaRF subregion boundaries, applicable plant taxa distribution string updates, and revised descriptions for these geographic areas were provided as updates and incorporated into the Jepson eFlora (http://ucjeps.berkeley.edu/eflora/), CCH (http://ucjeps.berkeley.edu/consortium/), and Jepson Online Interchange (http://ucjeps.berkeley.edu/interchange/) during September 2015.

DISCUSSION

The revised KR boundary now provides a far more accurate representation of the ecological and geologic attributes of this unique area. The new boundary also better portrays the distribution of many taxa that reach their northernmost California limits in the eastern KR and the occurrence of several endemic or near endemic taxa. This revised boundary and the associated descriptions are also congruent with other established geologic and geographic classification systems (e.g., Irvin 1994; Miles and Goudy 1997), reducing potential confusion when conducting various natural resource analyses in the eastern KR.

ACKNOWLEDGMENTS

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ARCHIDIUM CRASSICOSTATUM (ARCHIDIACEAE), A NEW AND LONG-OVERLOOKED SPECIES FROM CALIFORNIA, U.S.A.

David R. Toren, Kenneth M. Kellman, and James R. Shevock[1]
California Academy of Sciences, Department of Botany, 55 Music Concourse Dr., Golden Gate Park, San Francisco, CA 94118-4503
[1]jshevock@calacademy.org

Abstract

Archidium crassicostatum D.R. Toren, Kellman & Shevock is described and illustrated, and is currently known from two counties from California. It appears to be the sole species of the genus from the state and is well marked by its exceptionally wide costa, which can occupy as much as one-third the width of the leaf base. Previous reports of *Archidium alternifolium* (Dicks. ex Hedw.) Schimp. and *A. donnellii* Austin from California are actually *A. crassicostatum*. Details of habitat, ecology, and distribution are given and morphological distinctions among similar-looking but unrelated taxa are discussed.

Key Words: bryophytes, California Floristic Province, cleistocarpous mosses, Mediterranean climate, taxonomy.

The Archidiaceae are a monotypic family comprising about 30 species (Stone 2006) and a majority of these are found only south of the Tropic of Cancer (Snider 1975). *Archidium* Brid. is most abundant in Australia with 16 species (Stone 2006), Africa has 14 species (Magill 1981), Chile has two species (Müller 2009), and one species occurs on the Iberian Peninsula (Guerra and Brugués 2015). In North America, six species are known, but the genus is notably absent from the western part of the continent (Snider 1975).

Several species of the genus are poorly known. For example, in his worldwide monograph, Snider (1975) recognized 26 species, and at that time, 12 of these were known from three collections or less, and six species were known from less than ten collections each. Considering that a substantial number of species of the genus inhabit Mediterranean-type climate areas in Australia (Stone 2006), Chile (Müller 2009), South Africa (Magill 1981), and the Iberian Peninsula (Guerra and Brugués 2015), it is noteworthy that the genus was only recently detected in California, well known for its similar climate (Burge et al. 2016). Some explanations for this might be that the plants are very small, inconspicuous, and have a drab aspect. Also, most shoots in a colony lack sporophytes, and even when present they are difficult to see. Thus, *Archidium* may have been passed over as something unidentifiable and unworthy of collection.

The first verified California report of *Archidium* is from Santa Cruz County, identified as *A. alternifolium* (Dicks. ex Hedw.) Schimp. (Kellman 2003). Subsequently, the second author collected plants from this county in 2004. These collections formed the basis for the reference of *Archidium* in the state (Norris and Shevock 2004; Spence 2007; Malcolm et al. 2009; Burge et al. 2016). The genus was first discovered in Lake County, California in 2011 by the first author and Ed Dearing. These plants were initially determined as *A. donnellii* Austin, but with reservations regarding a number of morphological characters. Later, in 2015 two additional localities were reported from Lake County as *Archidium* sp. (Toren 2015). In the spring of 2016, plants were recollected from one locality in each of the above mentioned counties and this revealed that both populations were larger than previously thought.

In 2015, *Archidium* specimens from California were sent to William Buck at the New York Botanical Garden, who suggested the plants might be undescribed. Upon critical examination of more abundant material, we conclude these specimens do not conform to *A. alternifolium*, *A. donnellii*, or any other species treated in the worldwide monograph of *Archidium* (Snider 1975), or in the regional floras for the genus in Australia (Stone 2006), North America (Spence 2007), South Africa (Magill 1981), and Mexico (Sharp et al. 1994). A few additional species of *Archidium* have been described more recently, including *A. yunnanense* Arts & Magill (1994) from China and *A. oblongifolium* D. F. Peralta, A .B. M. Rios & B. Goffinet (2015) from Brazil. However, these species are morphologically very different from the Californian plants and appear to belong to other sections of the genus as defined by Snider (1975).

Taxonomic Treatment

Archidium crassicostatum D.R. Toren, Kellman & Shevock sp. nov. (Fig. 1).—TYPE: USA, California, Lake Co., Robin Hill near north shore of Clear Lake and south of Rodman Slough County Park, T15N, R9W, section 31, 39°06′30.1″N, 122°53′46.7″W 1350 ft., 1 May 2016, *Toren & Dearing 10400* (holotype: CAS; isotypes CONN, MO, NY).

FIG. 1. *Archidium crassicostatum* D.R. Toren, Kellman & Shevock. 1. Two fertile habits. 2. Three sterile habits. 3. Dissection showing capsule foot. 4. Opened capsule with spores. 5. Two perichaetial leaves. 6. Four cauline leaves. 7. Four basal leaves. 8. Apex of perichaetial leaf. 9. Apex of cauline leaf. 10. Basal leaf cells. 11. Sections through medial cauline leaves, base to apex. 12. Basal cells of perichaetial leaf. 13. Stem cross section. Scale bars: 1 mm, habits: 1–3; 150 μm, spores: 4; 0.25 mm, leaves: 5–7; 50 μm, cells: 8–13. All from *Toren & Dearing 10400*.

Diagnosis: The Californian plants can be differentiated from all members of *Archidium* by the plane, channeled leaves, the areolation of small, quadrate, thick-walled cells in many rows at the base of the vegetative leaves and strong costa which is broader than any other species of the genus.

Plants small, perennial by continuous production of branches, 3–5 mm high, green to yellow-green to dingy yellow-brown to tan, gregarious to loosely caespitose, when well developed forming turfs with the shoots occasionally becoming procumbent. **Stems** of the current season ± evenly foliate, simple to 2–3-branched, erect to stoloniferous, 1–2 sterile innova-

tions often produced in axils of perichaetial leaves. Stem cross section rounded, central strand present, inner cortical cells large, with thickened yellowish walls, outer cortical cells smaller and darker in color. **Rhizoids** smooth, pale grayish brown. Lower stem including buried portions dark brown to blackish, with chlorophyllous regenerative shoots having much reduced leaves. Lower stem leaves near soil level small, bract-like. **Upper stem leaves** when dry erect-patent with upper parts ± incurved, flexuose to erect and appressed, slightly spreading when wet, varying from deltoid-ovate to oblong-lanceolate to lanceolate, shortly to gradually acuminate, channeled, tubulose in upper one-fifth of leaf, 0.8–1.1 mm long, 0.3–0.4 mm wide, margins entire, plane. **Costa** 75–140 μm, somewhat broader at base, filling one-third of width of leaf, in cross section flattened to crescent-shaped, with adaxial cells only somewhat differentiated from the abaxial cells, stereids and differentiated guide cells absent, filling the acumen to shortly excurrent in a stout spine. Areolation ± uniform, cells firm-walled, ± thickened, yellowish. **Median and upper cells** mostly quadrate to occasionally short rectangular, 7.5(–10.0) × 7.5(–17.0) μm, somewhat bulging in cross section, sometimes bistratose in 1–2 rows juxtacostally. **Basal cells** quadrate in 12–16 rows from costa to margin, 7.5(–10.0) × 7.5(–10.0) μm. Alar cells not differentiated. Specialized asexual reproduction absent. Sexuality unconfirmed, perigonial buds and antheridia not seen. **Perichaetial leaves** erect to erect-spreading, concave, mostly broadly ovate or elliptic, acuminate, somewhat larger than stem leaves, sheathing the capsule, entire, not recurved; costa (125–)175–200 μm wide, excurrent in a stout spine; leaf cells in lower one-third of leaf hyaline with age, thin walled, rectangular, mostly 3:1 (6:1), cells in upper part of leaf firm-walled, irregular in shape, mostly 2:1. **Vaginula** spherical when young, becoming cup-shaped with an embedded bulbous foot. **Sporophytes** rare, 1 per stem, capsule globose, 350–550 μm in diameter, attached to foot, yellow with scattered black spots, seta none, exothecial cells irregular in shape, thin walled, stomata absent. **Spores** about 30 per capsule, spherical to ± polyhedral, hyaline to pale yellow, smooth to finely granulose, 150–160 μm in greatest dimension.

Paratypes: USA, CALIFORNIA, **Lake Co.**: Hidden Valley at end of Conestoga Road, 1400 ft., 11 February 2013, *Toren & Dearing 9994* (CAS); north shore of Clear Lake, Robin Hill south of Rodman Slough County Park, 1350 ft., 18 March 2015, *Toren 10328* (CAS), and 10 May 2015, *Toren & Dearing 10338, 10339* (CAS); meadow northwest of Boggs Lake, 2800 ft., 11 May 2015, *Toren & Dearing 10351* (CAS); northwest of Rodman Slough, inlet to Clear Lake upslope from road curve, 1340 ft., 1 May 2016, *Toren & Dearing 10405* (CAS); **Santa Cruz Co.**: Wilder Ranch State Park, off Englesman Loop Trail, 140 m, 6 March 2004, *Kellman 3531* (CAS) and same locality, 27 Mar 2016, *Kellman 8101* (CAS, CONN).

Taxonomic Relationships

According to Snider (1975), *Archidium* consists of four sections, based on various combinations of morphological characters which illustrate the principal divergent trends within the genus. Following this systematic concept, *A. crassicostatum* seems to belong in section *Phascoidea* G. Roth., which is defined by irregular areolation in the perichaetial leaves, thick-walled cells of the stem and innovation leaves, poorly differentiated alar cells, and as an apparent adaptation to drier habitats, julaceous to erect spreading leaves.

The new species is further characterized by a number of microscopic features, but since the plants are often encrusted or infiltrated with algae and soil particles, they should first be cleaned in hot water. When leaves are stripped from the stem and mounted, a large patch of stem cortical cells remains attached to the costa base (Fig. 1.10). This character also occurs in *A. elatum* Dixon & Sainsbury of Australia and New Zealand. Another microscopic feature is that the leaf basal cells, especially those of the costa, contain numerous, scattered, yellowish oil droplets.

Etymology

The name of the species derived from the Latin refers to the remarkably stout, broad costa.

Habitat and Ecology

Archidium crassicostatum is found in bare, sandy soil in sheet drainage areas, seasonally moist meadows, hillside seepages and trail banks mostly in clearings in chaparral and oak woodlands up to the Yellow Pine Forest. (500 to ca. 2800 ft.). The species is tolerant of extended hot and dry periods during the summer season. It seems to prefer moderately disturbed areas where native and non-native vegetation, especially grasses, have not completely invaded. Older stems within colonies sometimes become prostrate and buried, especially on sandy soils. Later, new shoots often arise from the leaf axils of moribund shoots (Fig. 1.2). Stone (2006) noted that several species of *Archidium* are efficient soil binders since the plants spread by repeated seasonal growth increments of fertile and sterile branches accompanied by abundant rhizoids. This phenomenon was observed on a small scale at the type locality of *A. crassicostatum*. Fruiting plants of the new species are generally rare in all populations and the capsules are very inconspicuous because they are mostly overtopped by surrounding innovation and perichaetial leaves (Fig. 1). Mosses often associated include *Bartramia aprica* Müll. Hal., *Ceratodon purpureus* (Hedw.) Brid., *Entosthodon californicus* (Sull. & Lesq.) H. A. Crum & L. E. Anderson, *Ephemerum serratum* (Schrad. *ex* Hedw.) Hampe, *Pleuridium acuminatum* Lindb., and *Tim-*

miella anomala (Bruch & Schimp.) Limpr. The liverworts *Cephaloziella divaricata* (Sm.) Schiffn., *Riccia campbelliana* M. Howe, and *R. trichocarpa* M. Howe occur in smaller quantities. Some associated vascular plants are *Arctostaphylos manzanita* Parry, *Baccharis pilularis* DC., *Eriogonum fasciculatum* Benth., *Eryngium* sp., *Juncus capitatus* Weigel., and introduced grasses.

DISTRIBUTION

Based on current data, *A. crassicostatum* is endemic to California and restricted to the Coast Ranges in Lake and Santa Cruz counties. It is highly probable the new species will be found in the intervening counties and additional searching in the California Floristic Province may reveal more localities, furthering a better understanding of its geographical distribution. Although it is a perennial moss, it is small and therefore more easily seen during the spring.

MORPHOLOGICAL DISTINCTIONS AMONG SIMILAR APPEARING TAXA

Fertile *Archidium crassicostatum* can be recognized immediately by the immersed, hidden spherical capsule with very large spores, in combination with the plane lanceolate leaves and broad costa. However, sterile plants could easily cause confusion. Comparison must be made with mosses with immersed capsules including *Acaulon* Müll. Hal., *Phascum cuspidatum* Hedw., *Ephemerum* spp., *Micromitrium* spp., and *Pleuridium* spp. Fortunately, all of these mosses produce capsules frequently. *Phascum cuspidatum* is easily separated based on its much broader leaves and papillose leaf cells. *Ephemerum* Hampe and *Micromitrium* Austin are much smaller plants whose capsules are almost always present and exposed. Furthermore, both have spores that are less than 120 μm. An apiculate capsule and persistent protonema further distinguish *Ephemerum* although its sporophyte is also hidden by the leaves, *Acaulon* is a bulbiform plant without the extended stem system of *Archidium*, and its spores are less than 50 μm. When capsules are present, *Pleuridium* Rabenh. is also easy to separate, since its capsules are exposed, ovoid with an apiculate tip and its spores are less than 50 μm. Without capsules, the two can be quite similar. Although they can share bistratose juxtacostal cells, the leaves of *Pleuridium* spp. are usually more subulate than *Archidium crassicostatum* and they have a distinct stereid band in the costa.

Because the distinct sporophyte is not easily seen in the field, *Archidium crassicostatum* somewhat resembles sterile forms of *Ceratodon purpureus* and a few species of *Didymodon* Hedw. and *Pseudocrossidium* R.S. Williams. All of these have exserted sporophytes, so fertile forms deserve no further mention. Sterile *Didymodon* can be immediately ruled out with the recurved leaf margins. Although the papillosity of *Didymodon* is often indistinct, it can always be detected at least on lateral view of the leaf margins. The revolute margins of *Pseudocrossidium* can be seen in the field if the leaves are wet, but when dry confusion is possible. A cross section of the leaf of *Pseudocrossidium* also reveals a strong stereid band.

The very plastic *Ceratodon purpureus* presents the largest challenge both macroscopically and microscopically. Usually, *C. purpureus* has recurved margins, which are irregularly serrulate near the apex. This normal form provides no difficulty in separation. However Burley and Pritchard (1990) allow for rarely entire and plane margins in their definition of the species. In this form, one must resort to a leaf cross section to see the stereid bands in the costa.

Separation from other species within *Archidium* nearly always requires sporophytes and perichaetial leaves. Snider (1975) emphases the position of the gametangia as a taxonomic character, but to date we have been unable to find antheridia in *A. crassicostatum*, thus its sexual condition remains unknown until antheridia are found. However, with the irregular perichaetial leaf areolation placing *A. crassicostatum* firmly in section *Phascoidea*, only comparison within that section is necessary (Snider 1975). Since the upper margins of *A. crassicostatum* are entire, *A. clavatum* I.G. Stone from Australia, *A. julaceum* Müll. Hal. from South America, and *A. julicaule* Müll. Hal. from Africa are eliminated because of their serrulate apices. Only the South African plants *A. muellerianum* Snider and *A. capense* Hornsch., have a costa as wide as 65–105 μm. *Archidium muellerianum* has papillose spores and narrowly recurved upper margins. *Archidium capense* has smooth spores like *A. crassicostatum*, but its costa is excurrent in a long awn. Neither has a costa well over 100 μm wide. All other *Archidium* in section *Phascoidea* G. Roth have narrower costae, between 30–85 μm wide (Snider 1975).

CONSERVATION IMPLICATIONS

Based on the limited number of occurrences discovered for *Archidium crassicostatum* during the past decade, we view this plant as relatively rare. Few of the occurrences are in habitats well protected on public lands. Since it is very inconspicuous during the dry season, it would be best to conduct surveys during winter and spring when the plants are actively growing and thus would be more easily noticed. In addition, the timing of winter rain is likely to influence whether a population is expressed each year. Very small soil mosses also frequently grow in mixed populations so they will need to be carefully examined microscopically since *Archidium* plants can occur as scattered individuals.

Edward Dearing who assisted with fieldwork, especially in collecting the type material. Three anonymous reviewers are acknowledged for carefully reading the manuscript and offering improvements. Lastly, we are grateful to Bill Buck for his examination of our earlier Californian *Archidium* collections and loan of the type of *A. elatum* for comparison purposes.

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CAMPYLOSTELIUM (PTYCHOMITRIACEAE) IN THE SOUTHWESTERN UNITED STATES: CAMPYLOSTELIUM LAEGERAE SP. NOV. AND C. PITARDII NEW TO THE AMERICAS

JOHN C. BRINDA
Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299
john.brinda@mobot.org

DAVID R. TOREN AND JAMES R. SHEVOCK
California Academy of Sciences, Department of Botany, 55 Music Concourse Dr., Golden Gate Park, San Francisco, CA 94118-4503

ABSTRACT

Two species of the genus *Campylostelium* Bruch & Schimp. are reported for the southwestern United States. **Campylostelium laegerae** Brinda, D.R. Toren & Shevock, sp. nov. is described and illustrated. *Campylostelium pitardii* (Corb.) E. Maier is reported as new to the Americas. Additional notes about the genus are provided, including a species key.

Key Words: *Campylostelium*, Mojave Desert, mosses.

INTRODUCTION

The bryoflora of some of the more remote parts of western North America is still relatively poorly known. Although recent floristic efforts in the region, particularly in California, have increased our knowledge considerably, much work remains to be done. Bryologists in the region still regularly report new distribution records and frequently encounter undescribed species. Clearly, basic floristic inventories and bryophyte taxonomy will continue to yield new and valuable information for some time to come.

It was during one such inventory project conducted by JRS for the bryophytes of Mojave Desert mountain ranges that the new species described here was discovered. This very small and inconspicuous moss was collected by Eve Laeger in November 2006, sent to California Academy of Sciences (CAS) for curation, and filed as "*Grimmia* sp." until it could be examined further. In June 2014, a study of desert *Grimmia* Hedw. collections was initiated by DRT and Laeger's collection proved to be perplexing. It did not resemble any *Grimmia* species known from western North America and eventually *Grimmia* was ruled out entirely. A similarity to *Ptychomitrium* Fürnr. was noticed by DRT but none of the smaller species of that genus are known to occur in California.

In July 2014 this specimen was sent to JCB for an opinion and *Ptychomitrium* was ruled out. Since the original collection did not contain many fruiting plants, JCB revisited the locality in April 2015 to assess the population. With the examination of more robust material it became clear that the plants represented an undescribed species, but the proper genus for it remained elusive. In March 2016 the area was again visited by JCB in order to determine if the species was restricted to a single canyon or possibly more widespread. A nearby canyon on the eastern slope of the range was surveyed and the new species collected there as well.

On the return trip to Las Vegas, JCB briefly stopped at Emigrant Pass to survey for the new species and instead discovered the first California population of *Campylostelium pitardii* (Corb.) E. Maier! A find all the more remarkable since the stop was planned hastily only after lingering too long over a milkshake at the China Ranch Date Farm. Having recently agonized over the determination of the Arizona plants also reported here, the California population was recognized immediately by JCB. Examination of the new species alongside *C. pitardii* under the microscope made their similarities apparent. As a result, we are now pleased to name this new species of *Campylostelium* Bruch & Schimp. after Eve Laeger.

TAXONOMIC TREATMENT

Campylostelium laegerae Brinda, D.R. Toren & Shevock, sp. nov. (Fig. 1).—TYPE: USA, California, Inyo Co., BLM California Desert District, Nopah Range Wilderness, northern Nopah Range, along an unnamed wash southwest of Pahrump Peak, 36.095219°N, 116.151873°W, 1193.5 m, 31 March 2015, *Brinda 7339* (holotype: MO; isotypes: CAS, NY).

Plants very small, usually 2–3 mm tall, in dense turfs, glossy, dark green to blackish where exposed to the sun, light brown upon senescence. **Stems** erect with frequent branching below the inflorescences; central strand well-developed; rhizoids reddish brown, smooth; axillary hairs hyaline, 4–5 cells long, rectangular to cylindrical, with the basal 1–2 cells shorter than the rest. **Leaves** about 1 mm long, erect to incurved when dry, spreading to recurved from a loosely sheathing ± erect base when wet, oblong-lanceolate with the base slightly broadened; margins erect and entire or obscurely notched; apex blunt and ± cucullate; costa single, strong, subpercurrent to
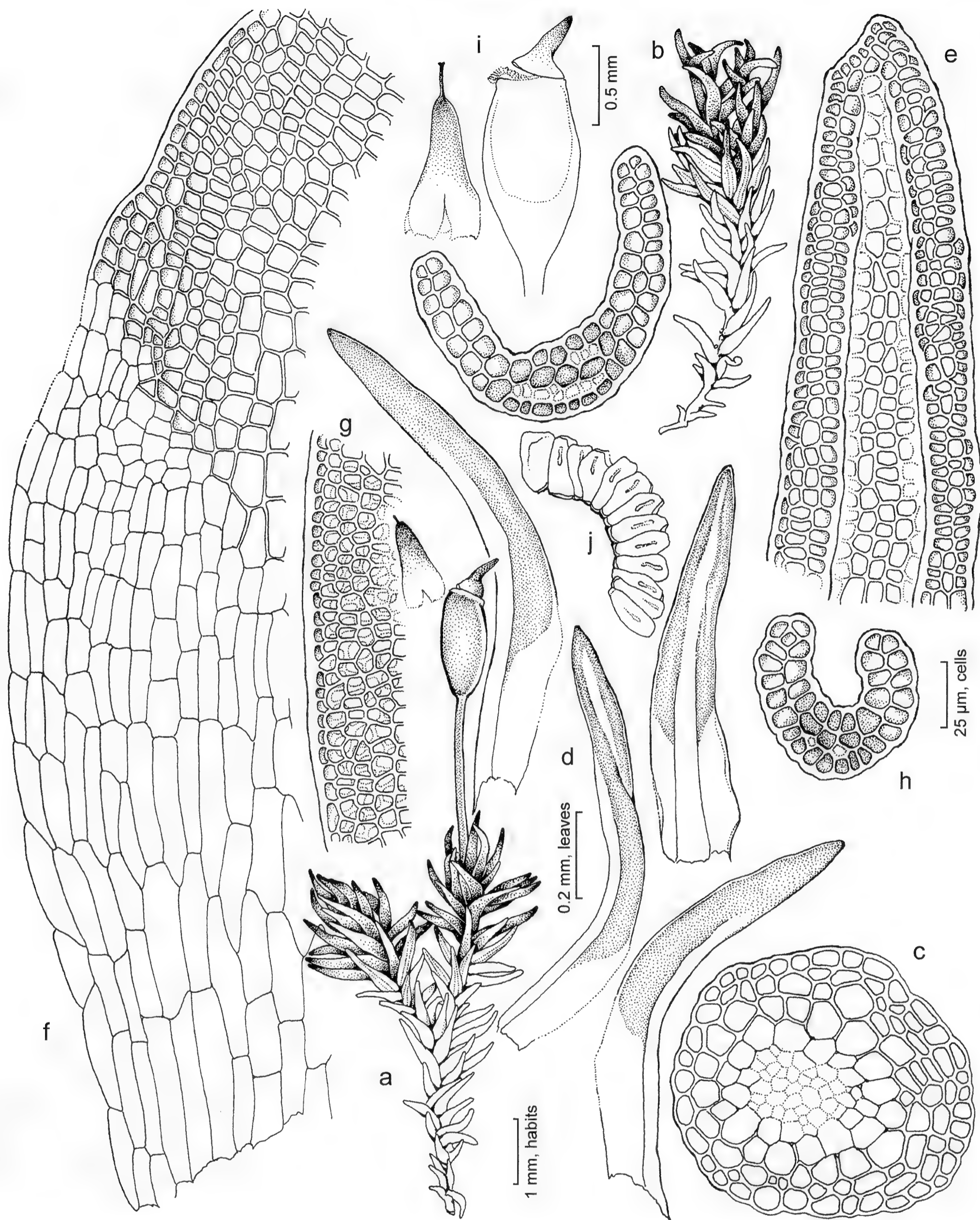
FIG. 1. (a-j) *Campylostelium laegerae*, California, *Brinda 7339* (MO): (a) fruiting plant, wet; (b) dry habit; (c) stem transverse section; (d) four cauline leaves; (e) leaf apex; (f) leaf basal cells; (g) marginal cells at mid-leaf; (h) two transverse sections of leaf; (i) capsule with dehiscent operculum and calyptra; and (j) portion of annulus.

percurrent, guide cells in a single layer with both dorsal and ventral bands of thin-walled tissue present proximally; upper laminal cells small, ± isodiametric, 8–12(–15) μm wide, entirely bistratose, smooth but with the cell walls more strongly thickened on the external surfaces; basal cells ± strongly differentiated, elongate, hyaline, and often running up the margins in one to several rows. **Specialized asexual reproduction**

apparently absent. **Sexual condition** autoicous, fruiting stems commonly gonioautoicous but many stems also exclusively male. **Perigonia** gemmiform, subtended by much shorter and broader leaves. **Perichaetia** terminal, perichaetial leaves neither highly modified nor strongly sheathing. **Seta** single, straight, smooth, about 1 mm long, centrally inserted. **Capsule** less than 1 mm long, erect, exserted, light brown, ovoid,

wrinkled or obscurely ribbed when dry; stomata present proximally on capsule, phaneropore; exothecial cells mostly elongate; annulus large, of 2–3 rows of oblong cells, somewhat persistent; operculum rostrate; peristome absent. **Calyptra** 0.6–0.7 mm long, mitrate, shallowly lobed at the base, naked, not plicate. **Spores** spheric, 12–15 μm, weakly roughened.

Paratypes: USA, CALIFORNIA. **Inyo Co.**: BLM Desert Conservation Area, Nopah Range, Nopah Range Wilderness, west slope of Pahrump Peak, T23N, R8E, section 18, 36°05′45″N, 116°09′25″W., 4000 ft., 30 Nov 2006, *Laeger 3624 & 3625* (CAS); along an unnamed wash southwest of Pahrump Peak, 36.093296°N, 116.157713°W, 1029.7 m, 31 Mar 2015, *Brinda 7316* (CAS, MO, NY); 36.094113°N, 116.153552°W, 1115.1 m, 31 Mar 2015, *Brinda 7330* (MO); along an unnamed wash northeast of Pahrump Peak, 36.101437°N, 116.133855°W, 1309.0 m, 23 Mar 2016, *Brinda 8450* (CAS), *8451* (NY), *& 8452* (MO).

Campylostelium laegerae is an inconspicuous moss that is likely to be overlooked in the field due to its superficial similarity to other small, blackish desert mosses such as *Didymodon australasiae* (Hook. & Grev.) R.H. Zander and epilose forms of *Grimmia moxleyi* R.S. Williams. Both of these mosses occur in abundance where the new species has been found, but the small, exserted capsules of *Campylostelium laegerae* set it apart from these and other associated species. The distinctive capsules of *C. laegerae* mature in late spring and are quite fragile, becoming easily broken when dry. The small, acrocarpous habit of the plants might suggest placement among the genera of the Pottiaceae but the smooth cells and lack of differentiated stereid bands in the costa exclude most of these possibilities. Under the microscope, the gametophytes bear some resemblance to species of *Ptychomitrium* such as *P. incurvum* (Schwägr.) Spruce. However, the plants are much smaller, and this combined with the small, mitrate, and shallowly lobed calyptra, suggest they are better placed in the genus *Campylostelium*.

THE GENUS *CAMPYLOSTELIUM* BRUCH & SCHIMP. 1846.

Campylostelium is traditionally regarded as a member of the Ptychomitriaceae, a small family of acrocarpous mosses currently viewed as containing six genera (Goffinet et al. 2009). Some members of the Ptychomitriaceae have recently been transferred from the Grimmiaceae such as *Indusiella* Broth. & Müll. Hal. and *Jaffueliobryum* Thér. (Hernández-Maqueda et al. 2008). Hernández-Maqueda et al. (2008) recommended the recognition of a monogeneric family Campylosteliaceae based on molecular data. More recent evidence however, suggests that *Campylostelium* should be retained within a more broadly circumscribed Ptychomitriaceae (Fedosov et al. 2016 [in press]). As recognized here, *Campylostelium* consists of five taxa widely scattered across North America, Europe, Asia,

and Africa. *Campylostelium* has also recently been discovered in South America (Ireland et al. 2006).

The new species is unique in several ways within *Campylostelium*. A narrow circumscription of the genus would exclude *C. laegerae* based on its erect-incurved leaves, straight seta, and eperistomate condition. However, given the recent inclusion of *Campylostelium pitardii* in the genus (see below under discussion of *C. pitardii*), its circumscription must be drawn more broadly. Both *C. pitardii* and *C. laegerae* have leaves that are erect-incurved rather than crispate when dry and *C. strictum* Solms is most easily separated from *C. saxicola* (F. Weber & D. Mohr) Bruch & Schimp. by its straight seta. The most vexing problem regarding generic placement of the new species is its eperistomate condition. However, peristome reduction is also known to occur in the genus (see note below on *C. saxicola* var. *brachycarpum* Nog.) and the sporophytes, though somewhat smaller, are otherwise quite similar to those of *Campylostelium saxicola* and *C. strictum*.

HABITAT, ECOLOGY, AND DISTRIBUTION

Currently, *C. laegerae* is known from desert mountain shrublands on sediment accumulating in the crevices of carbonate rocks at moderate elevations (1000–1300 m). It is documented from canyons below Pahrump Peak in the northern Nopah Range, Inyo County, California. The plants, when dry, become even more difficult to recognize while conducting surveys because of their minute size and dark coloration. They may blend in with shade in rock crevices and therefore can easily be overlooked. The occurrence of carbonate rock within desert scrub vegetation is a common feature of the Mojave Desert and we expect additional populations will be discovered. The limestones and dolomites of the northern Nopah Range are mostly Paleozoic in age and related geologic strata also occur in other mountain ranges in the region (Hazzard 1937, 1954; Stewart 1970). It may be helpful to seek out similar geological formations and substrates when searching for additional populations. Based on what is known, *C. laegerae* is apparently rare and localized in its distribution, but not currently threatened. The documented localities near Pahrump Peak occur within a federally designated wilderness area.

Etymology: Named in honor of Eve Laeger, a prolific collector of western North American bryophytes and CAS field associate. Two of her collections initially brought this species to our attention and prompted further investigation.

CAMPYLOSTELIUM PITARDII NEW TO THE AMERICAS

Campylostelium pitardii (Fig. 2) is a rare species occurring throughout the Mediterranean region, including southern Europe, North Africa, and the Middle East. Here we report it from the deserts of

both Arizona and California. Its discovery in two widely separated and largely undisturbed localities suggest that it is also a native component of the North American flora. Widely disjunct distributions are fairly common in bryophyte species, including well-known examples of western North American-Mediterranean disjuncts (Schofield and Crum 1972). Shaw et al. (2003) studied some of these intercontinental disjunct populations and concluded that they are apparently linked via recent long-distance dispersal events. The fact that bryophytes both reproduce sexually via spores and have numerous adaptations for asexual propagation probably increases the likelihood that these events will lead to successful establishment. Both American populations of *C. pitardii* possessed abundant sporophytes; *C. laegerae* in contrast is less fertile.

The American plants of *C. pitardii* were compared to several accessions (all at MO) of *C. pitardii* from the Mediterranean region (France, Spain, and Turkey) and found to be morphologically indistinguishable. *Campylostelium pitardii* is discussed and illustrated in several Mediterranean floras (e.g., Heyn and Herrnstadt 2004; Casas et al. 2006; Brugués and Ruiz 2015), and also by Maier (1998) who followed Herrnstadt et al. (1982) in placing *Grimmia gibbosa* Agnew (Agnew 1973; Agnew and Vondráček 1975) as a synonym and also made the combination in the genus *Campylostelium*. Greven (2003) doubted the placement of this species within the genus *Campylostelium*, but it has since been confirmed using molecular methods (Hernández-Maqueda et al. 2007, 2008, Fedosov et al. 2016 [in press]).

It is surprising that both Californian *Campylostelium* species were discovered within the same mountain range only 25 km apart from one another. However the geology of the two localities is somewhat different and the two species occupy separate niches. Greven (2003) described the habitat for *C. pitardii* in the Mediterranean region as partially shaded calcareous soils between shrubs. The American plants of *C. pitardii* occupy a similar niche, except that adjacent cliff faces provide the shade at both localities. In contrast, *C. laegerae* is a rock dwelling species that occurs in crevices and on ledges that are inclined to vertical in orientation. Both of these species apparently prefer calcareous substrates.

Specimens examined: USA, ARIZONA, **Mohave Co.**: BLM Arizona Strip District, Grand Canyon-Parashant National Monument, Parashant Canyon Narrows, 36.155415°N, 113.332383°W, 774.0 m, 29 Jun 2007, *Brinda 2020* (MO, UNLV); CALIFORNIA, **Inyo Co.**: BLM California Desert District, South Nopah Range Wilderness, southern Nopah Range, north-facing wash southwest of Old Spanish Trail at Emigrant Pass, 35.882859°N, 116.067336°W, 840.1 m, 24 Mar 2016, *Brinda 8463* (CAS, MO, NY).

ON *CAMPYLOSTELIUM SAXICOLA* VAR. *BRACHYCARPUM* NOG.

Noguchi (1950, 1988) described and illustrated a variety of *Campylostelium saxicola* from Japan based on its somewhat reduced peristome relative to the typical European plants. Iwatsuki et al. (1999) elevated this variety to the status of species (i.e., *Campylostelium brachycarpum* [Nog.] Z. Iwats., Yuk. Tateishi & Tad. Suzuki) and noted the presence of both taxa in Japan as well as North America. This problem has not yet been taken up by American authors (e.g., Reese 2007) and we have not examined enough specimens to come to any conclusion. However, given the discovery of an eperistomate member of *Campylostelium*, the problem of peristome reduction in the genus is now perhaps more interesting. The variety *brachycarpum* seems to be the more common one in North America. It is illustrated in Crum and Anderson (1981), whereas the typical variety seems to be illustrated in Ireland (1982). We recommend segregating the two entities as varieties until more information becomes available.

KEY TO THE RECOGNIZED TAXA OF *CAMPYLOSTELIUM*

1. Leaves highly polymorphic, from lingulate and rounded obtuse to oblong-lanceolate and gradually acuminate, sometimes terminating in a long, somewhat flexuose subula, lamina mostly unistratose with occasional small bistratose patches, margins not thickened; capsules emergent, asymmetric, gibbous at base . . . . *Campylostelium pitardii*
1. Leaves, aside from considerable variation in size, ±similar in shape, regularly bistratose, but often only on the margins; capsules exserted, symmetric, ovoid to cylindrical 2
    2. Leaves erect-incurved when dry, not crispate or circinately curled, uniformly bistratose across the entire lamina, margins not thickened; peristome absent . . . . *Campylostelium laegerae*
    2. Leaves loosely crispate to circinately curled when dry, typically bistratose on the margins or sometimes also in patches on the distal lamina; peristome present 3
        3. Leaf margins thickened in 2–3 rows; costa >60 μm wide at base; seta straight when hydrated . . . . *Campylostelium strictum*
        3. Leaf margins thickened in 1–2 rows; costa <50 μm wide at base; seta curved when hydrated 4
            4. Peristome somewhat reduced, the teeth widely spaced and undivided, sometimes nodose . . . . *Campylostelium saxicola* var. *brachycarpum*
            4. Peristome well-developed, the teeth closely set and divided into slender segments . . . . *Campylostelium saxicola* var. *saxicola*
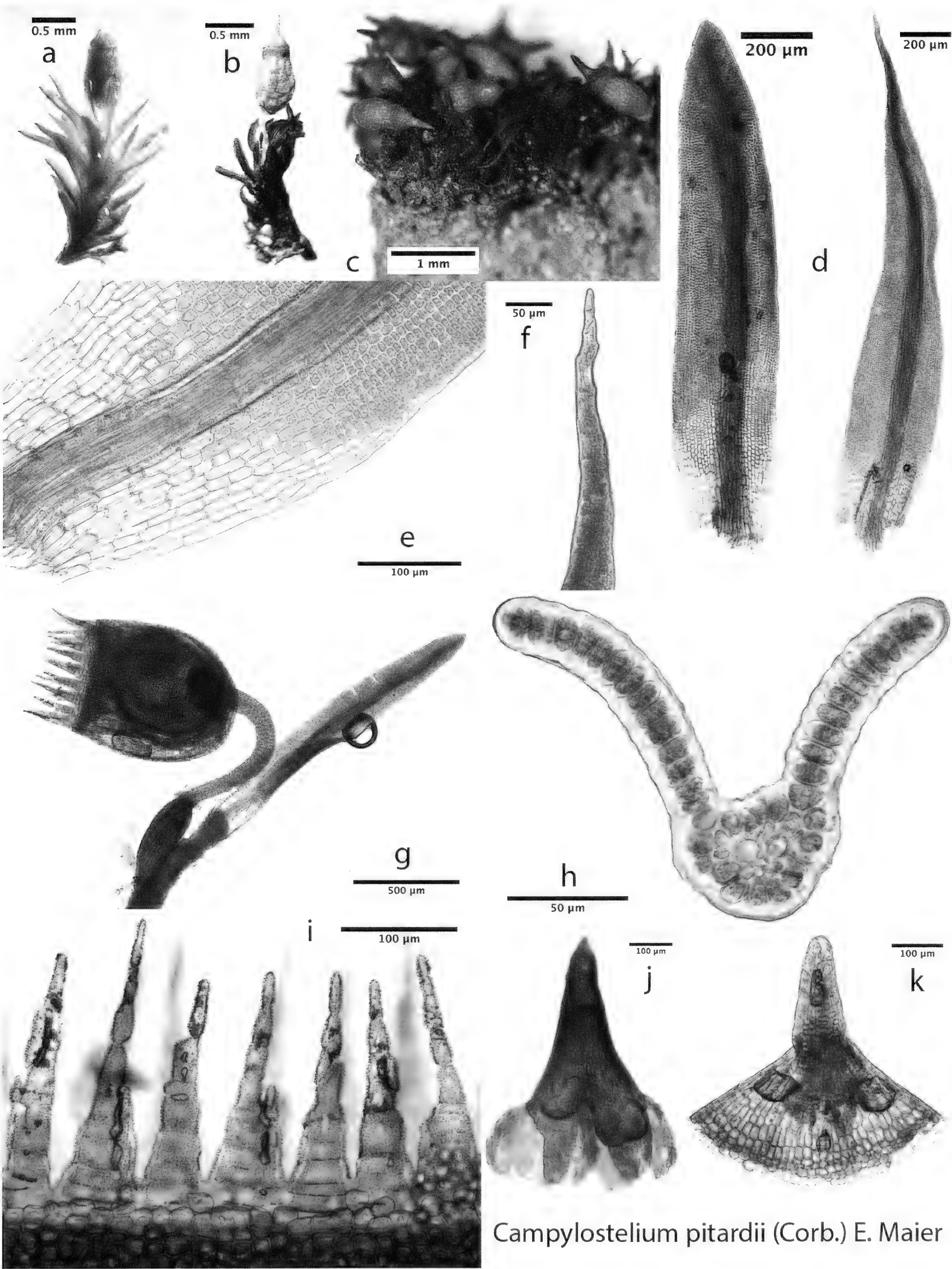
FIG. 2. (a-k) *Campylostelium pitardii*, California, *Brinda 8463* (MO): (a) fruiting plant, wet; (b) the same, dry; (c) small portion of population; (d) two cauline leaves showing dimorphism; (e) leaf basal cells; (f) apex of acuminate leaf; (g) capsule, wet; (h) transverse section of leaf; (i) peristome teeth; (j) calyptra; and (k) operculum.

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DUDLEYA HENDRIXII A NEW, RARE SPECIES FROM COLONET MESA, BAJA CALIFORNIA

STEPHEN WARD MCCABE

Environmental Studies Department and the Arboretum, University of California, Santa Cruz, CA 95064
smccabe@ucsc.edu

MARK W. DODERO

RECON Environmental Inc., 1927 5th Avenue, San Diego, CA 92101

MICHAEL G. SIMPSON

Department of Biology, San Diego State University, San Diego, CA 92182

ABSTRACT

Dudleya hendrixii S. McCabe & Dodero is a succulent endemic, restricted to a small area of Colonet Mesa (Baja California, Mexico). It is similar to the more widespread *D. blochmaniae* (Eastw.) Moran subsp. *blochmaniae,* which has been placed in subg. *Hasseanthus* (Rose) Moran, and to *D. attenuata* (S. Watson) Moran subsp. *orcuttii* (Rose) Moran, which has been placed in subg. *Stylophyllum* (Britton & Rose) Moran. Both of these other species have much wider ranges. *Dudleya hendrixii* differs from *D. blochmaniae* subsp. *blochmaniae* in having fewer, terete, more upright, and waxier leaves. Unlike *D. attenuata* subsp. *orcuttii, D. hendrixii* is summer deciduous, acaulescent, and has much shorter inflorescences.

RESUMEN

Dudleya hendrixii S. McCabe & Dodero es suculenta. *Dudleya hendrixii* es endémico a una pequeña porción de la mesa Colonet. Es similar a la *D. blochmaniae* (Eastw.) Moran subsp. *blochmaniae,* que se ha colocado en el subgenera *Hasseanthus* (Rose) Moran, y *D. attenuata* (S. Watson) Moran subsp. *orcuttii* (Rose) Moran, que se ha colocado en el subgenera *Stylophyllum* (Britton & Rose) Moran, las cuales tienen rangos más extensivos. Se distingue *Dudleya hendrixii* de *D. blochmaniae* subsp. *blochmaniae* por la presencia de menos hojas, que son más verticales, cilíndricos, más vertical, y las hojas más cerosas. A diferencia de *D. attenuata* subsp. *orcuttii, D. hendrixii* es de hoja caducifolio verano, casi sin tallo, y tiene inflorescencias mucho más cortos.

Key Words: Colonet, Crassulaceae, Dudleya, Jimi Hendrix, new species, rare.

The genus *Dudleya* Britton & Rose (1903) consists of approximately 47 species of leaf-succulent perennials, native to California, Oregon, Arizona, Nevada, and Utah, USA, and to Baja California, Baja California Sur, and Sonora, Mexico (Wiggins 1980; Dodero and Simpson 2012; McCabe 2012). *Dudleya* subg. *Hasseanthus* (Rose) Moran, as traditionally treated (Moran 1950, 1951, 1953; Munz 1974; Bartel 1993; McCabe 2012), contains six species (seven taxa total): *D. blochmaniae* (Eastw.) Moran subsp. *blochmaniae, D. blochmaniae* subsp. *insularis* (Moran) Moran, *D. brevifolia* (Moran) Moran, *D. crassifolia* Dodero & M.G. Simpson, *D. multicaulis* (Rose) Moran, *D. nesiotica* (Moran) Moran, and *D. variegata* (S. Watson) Moran. Species in subg. *Hasseanthus* are characterized by their drought deciduous leaf duration and hypogeous caudex, and range from San Luis Obispo Co., California to northern Baja California, Mexico.

Small *Dudleya* plants on Colonet Mesa were mentioned in Thomson (1993), Clark et al. (2008), Dodero et al (2009), and in Harper et al. (2011). One taxon from Colonet Mesa was named *D. crassifolia* Dodero & M.G. Simpson (2012), differing from other members of subg. *Hasseanthus* by having a "thicker petiole," (2–3.3 mm thick vs. 0.4–1.7 mm thick in other subg. *Hasseanthus* taxa) and "conspicuous dried leaf bases persisting on the caudex." Here we describe another form from Colonet Mesa and discuss its possible position within the subgenus. This form of *Dudleya* should be treated as a new species using a taxonomic (morphologic) species concept (Cronquist 1978, 1988), in which species are circumscribed based on the discontinuity of morphological features.

TAXONOMIC TREATMENT

Dudleya hendrixii S. McCabe & Dodero, sp. nov. (Figs. 1–3).—Type: MEXICO, Baja California, Colonet Mesa, ca. 18 km miles south-southwest of Colonet, growing in clay soils in a large, shallow depression within a mesa top, between very occasional nearby mounds, the mounds several cm to dm higher, 95 meters elevation, 30°57.608′ N, 116°19.449′ W, 3 June 1995, *M. Dodero s.n.* (holotype: SD; isotypes: BCMEX, RSA, SBBG, UC).

Dudleya hendrixii is similar to *D. blochmaniae* subsp. *blochmaniae,* differing in having fewer, terete,
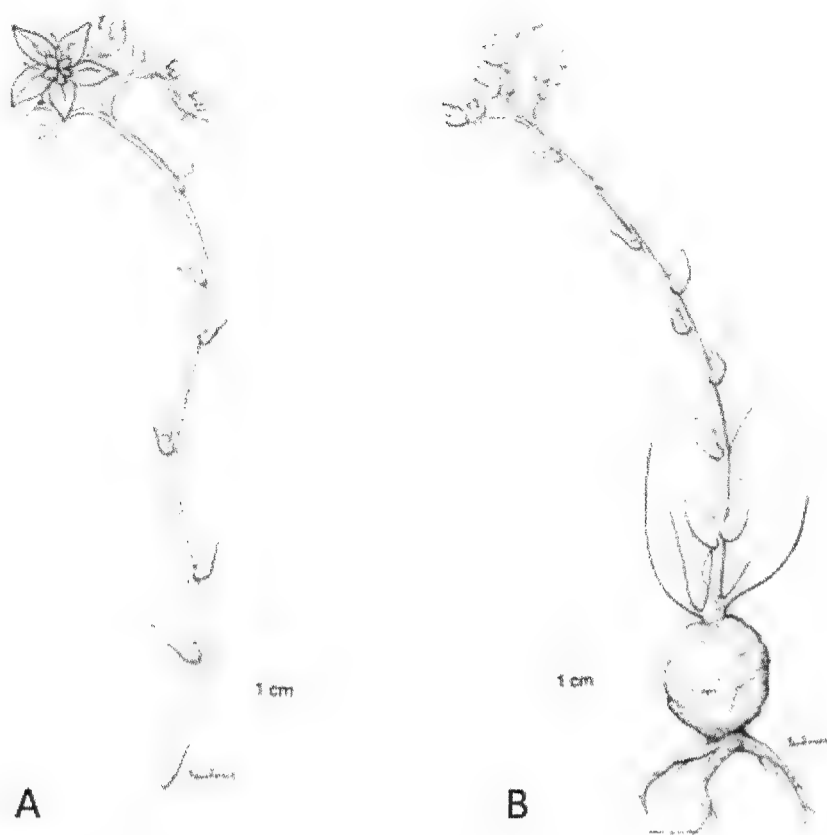
FIG. 1. Illustrations of *D. hendrixii*. A. Inflorescence, showing alternate peduncle bracts and spreading petals of flower. B. Whole plant, showing corm-like structure and basal leaves, this sample with single inflorescence. Line drawings by Becca Berezuk.

more upright, and waxier leaves. It is similar to *D. attenuata* (S. Watson) Moran subsp. *orcuttii* (Rose) Moran [=*D. attenuata* (S. Watson) Moran *sensu* Moran 2001, differences between the subspecies are discussed in McCabe, in prep.], differing in being summer deciduous and acaulescent and in having much shorter inflorescences.

Plants unbranched, low, succulent, to ca. 5 cm across. **Caudex** essentially acaulescent, very short, corm-like, spherical to slightly longer than wide, at ground level. **Leaves** in a rosette, usually 3 to 5, summer deciduous, leaf bases not buried, succulent, ± circular in cross-section, linear to fusiform, straight or curved, almost always with a medium amount of light gray glaucescence, upright, typically with one leaf curving over the apex of the plant, upper portions of leaves not close to one another, apex acuminate-attenuate, not angled by bud printing. **Inflorescences** 2–4 from caudex, erect to ascending, 10–20 cm tall (up to 25 cm in cultivation), typically with several lateral branches 1–2.5 cm long, peduncle 1–2 mm thick, flecked with barely visible tiny short vertical red lines (previous year's dead peduncles persistent in cultivation and light colored), lowest two bracts often sub-opposite, those above almost always alternate, lower bracts 4–10 mm long, 3–7 mm wide, 3–5 mm thick, pyriform and flattened above, apex attenuate, almost always glaucous (plump in late June in cultivation). **Pedicels** 0–1 mm long. **Flower.** Calyx ca. 3 mm long, sepals red-brown ± glaucous especially toward base. Corolla ca. 8 mm long, 3 mm wide, petals spreading to inclined (to 25° above horizontal), in bud pink, at maturity white with pink especially on abaxial side, red along keel, odor not noted in the wild (odor absent in a sample size of four plants in cultivation). **Stamen** filaments ca. 6 mm long, anthers ca. 0.5 mm

long, basifixed, predehiscent anthers red, pollen yellow. **Gynoecium** 6–7 mm long, pistils white when young, spreading, becoming widely spreading at maturity. **Fruits.** Follicles 3–4 mm long, widely spreading.

Paratype: MEXICO, BAJA CALIFORNIA. Colonet Mesa, ca. 18 km south-southwest of Colonet, 96 meters elevation, 30°57.608′N, 116°19.449′W, 4 August 2009 ex hort., *S. McCabe 1237* (BCMEX, UC).

DISTRIBUTION, ABUNDANCE, AND HABITAT

There are approximately 5,000–10,000 plants distributed over a few acres of land. Colonet Mesa has a coastal maritime influence. Some of the associated species found near *D. hendrixii* include *Agave shawii* Engelm., *Calochortus splendens* Douglas ex Benth., *Crassula connata* (Ruiz & Pav.) A. Berger, *Cuscuta* sp., *D. ingens* Rose, *Euphorbia misera* Benth., *Ferocactus viridescens* (Torr. & A. Gray) Britton & Rose, *Lasthenia* sp., *Linanthus dianthiflorus* (Benth.) Green, *Lycium brevipes* Benth., numerous lichens, a *Gnaphalium* L. or *Pseudognaphalium* Kirp. (identified from photos), and a few small grasses. *Dudleya hendrixii* occurs within a very large, comparatively flat coastal mesa having some vernal pools. The most common vegetation type away from the pools is referred to as maritime succulent scrub (*mattoral rosetofilo costero*) (Harper 2011) or as Martyrian coastal succulent sage scrub (Dodero et al. 2009). *Dudleya hendrixii* is found in a single, large, shallowly concave, slight depression that is, however, not a vernal pool. This depression has a fairly gentle slope that may have surface water flowing into it during heavy rains. Within this shallow depression are low mounds ca. 0.3–1.5 m high. Various drought-adapted species occur on the mounds, including *Agave shawii* subsp. *shawii, D. ingens,* and *D. attenuata* subsp. *attenuata,* which are not abundant off of the mounds.

PHENOLOGY AND HERBIVORY

Dudleya hendrixii flowers in the wild from late May to June. After a brief survey on 23 March 2009, one plant showed signs of damage from the larvae of a moth or butterfly. At that time lower bracts were visible, but no flower buds. In cultivation in a common garden, *D. hendrixii* flowered much later than *D. blochmaniae* subsp. *blochmaniae.*

ETYMOLOGY

The specific epithet, *hendrixii*, is named after the famous American guitarist Jimi Hendrix. Music by that artist was playing when the second author first saw the plants.

Suggested common name: Hendrix's Dudleya.
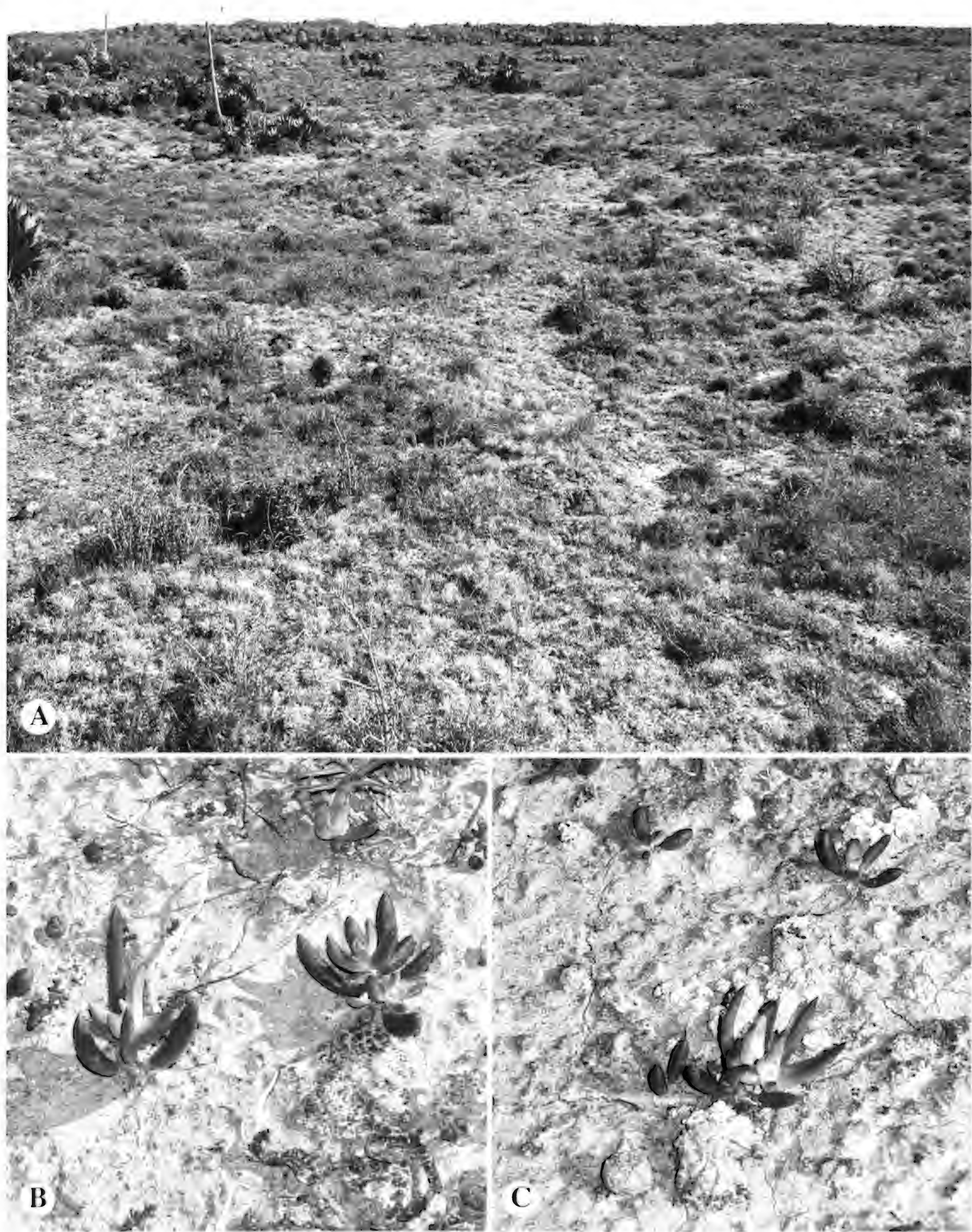
FIG. 2. Photographs of *D. hendrixii* in the field, at Colonet Mesa. A. Vegetation. Note topographically lower areas near foreground with surrounding intermittent mounds. B-C. Individual plants at young stage. Note vegetative leaves arching over young inflorescence.

Table 1. Comparison of four *Dudleya* taxa that occur in the Colonet Mesa region.

	D. hendrixii	*D. blochmaniae* subsp. *blochmaniae*	*D. crassifolia*	*D. attenuata* subsp. *attenuata* (occurs with *hendrixii*) and *D. a. orcuttii* (which occurs elsewhere on the Mesa)
Summer deciduous	Obligate	Obligate	Some are not obligate, perhaps some are	No
Obvious above ground stem?	0	0	0, base of leaves buried	Yes
Number of leaves	Usually 3–5	Usually more than 5	Usually 5 or more	More than 5
Conspicuous dried leaf bases persisting on the caudex	Rare or uncommon	No	Usually	Yes, on an above ground stem
Petal color	White, keel red	White, keel red	White, "keel and base maroon, often suffused with maroon throughout." The red of *D. hendrixii* is the same as the maroon of *D. crassifolia*	White or yellow, usually with red to brownish-red keel
Leaf attitude	Lvs ± upright with one often arching over the apex	Leaves spreading	Leaves ascending	Lvs ± upright, with none or one or more arching over the apex
Waxiness of rosette leaves	Fairly waxy, greyish-white	None to slight.	Variable	Fairly to very waxy
Leaf color	Greyish white	Green to bronze (red-brown) with slight waxiness	Variable	Greyish white to white [to purple-grey or purple-red]
Leaf attitude	Mostly upright, often with one curving over apex	Spreading to lax, no leaves curving over apex	Usually ascending, no leaves curving over apex	Ascending to upright, no leaves curving over apex [or rarely so]
Petiole	Not twisted ¼ turn as leaf blade bends towards substrate; narrow (1–1.5 mm), upright	Sometimes twisted ¼ turn as leaf blade bends towards substrate; distinctly narrow (<1mm), lax	Not twisted ¼ turn as leaf blade bends towards substrate; leaf blade slightly wider than petiole, fairly upright	Not twisted ¼ turn as leaf blade bends towards substrate; no obvious petiole at 1f diameter < 3 mm, i.e. no constriction indicating a distinct petiole, upright
Petiole diameter in mm	1.5–2.0	<1, to 1.0	[1.5–] 2.0–5.0	[2.5–] 3–5.5
Inflorescence length	Usually <10 (to 25 cm in cultivation)	(0.9) 3–12 (–22) cm	6–17 cm tall	5–25 cm
Leaf shape	Fusiform and ± falcate	Long, club-shaped	Short, club-shaped	Linear to falcate and terete
Leaf apex	Acute, pointed, not rounded	Acuminate, blunt and rounded	Acuminate, blunt and rounded, (angled by bud printing, at least at first)	Acute, pointed, not rounded
Habitat	In a shallow, depression on a mesa, the habitat having the appearance of it being a remnant vernal pool. The depression may have slightly more moisture after rains than surrounding areas. On clay soils near coast. With *Lasthenia*, but not on the slightly higher ground with *Agave shawii*, or *D. ingens*	Various, including sandy flats in *Lasthenia* flower fields at Colonet Mesa, but often in shallow soils on mesa tops and rocky outcrops. Variable, including with red concretions and on clay soils.	Shallow soils on mesa tops with iron-rich nodules/concretions with little other vegetation.	Where it is in closest proximity to the *D. hendrixii*, it is on raised mounds of soil that harbor drier vegetation, including, *Ferocactus, Agave shawii,* and *D. ingens*

TABLE 1. CONTINUED

	D. hendrixii	D. blochmaniae subsp. blochmaniae	D. crassifolia	D. attenuata subsp. attenuata (occurs with hendrixii) and D. a. orcuttii (which occurs elsewhere on the Mesa)
Rosette flat topped and compact	0	0	X	0
# of rosettes	1	1	1 to several	Few to usually many
Length of floral tube	0–1 mm	3 mm	2 mm	3 mm
Leaf base	Exposed (or only very slightly buried?)	Exposed (or only very slightly buried)	Usually buried	Exposed on above ground stem
Corm-like caudex	Globose, spherical to slightly longer than wide	Elongate	Cylindrical to irregular	Absent
Lower bracts	Almost always very waxy	No wax or slightly waxy (more wax in D. b. insularis)	Waxy or not. Often more waxy at the bases of the bracts than above	Waxy
Flowering	May-June (Late June-early August in cultivation)	March-June. Two of four plants in common garden completely finished flowering before any flowers opened on D. hendrixii	Approximately May-June	Approximately April-June
n =	Unknown	17, 34, 51	34	17, 34

FIG. 3. Photographs of *D. hendrixii* from cultivated material. Note succulent, fusiform leaves (above) and spreading petals of flowers (below).

DISCUSSION

Taxonomic Relationships

If the subgenera of *Dudleya* continue to be recognized (see Yost et al. 2013 for discussion), then *D. hendrixii* is cautiously placed in the subg. *Hasseanthus* based on its underground corm-like caudex, essentially acaulescent stem habit, widely spreading white petals marked with red or pink on the keels, and widely spreading mature follicles. The new species differs from other taxa in several characters (Table 1). There is another unnamed form or species also occurring on Colonet Mesa, not included in Table 1, that is intermediate in some ways between *D. crassifolia* and *D. attenuata*. Further work is needed to determine if it should be recognized taxonomically.

Although a number of *Dudleya* taxa can be crossed one with the other artificially or in nature (Moran 1978; McCabe unpublished), and presumably the same would be true in *D. hendrixii,* differences in habitat among these taxa might explain why no introgression has been observed in the wild. Other factors might maintain separation between *D. hendrixii* and other species in the wild. Differences in floral morphology between *D. hendrixii,* with widely spreading petals, and *D. ingens,* with upright petals, suggest quite different pollinators may be involved. This may make hybridization uncommon. In cultivation with thousands of other *Dudleya*, most of which do not occur with *D. hendrixii* in nature, open pollinated members of *D. hendrixii* appeared to have produced hybrid offspring (McCabe personal communication). Reproductive isolation between *D. hendrixii* and *D. blochmaniae* subsp. *blochmaniae* is possibly maintained in the wild by some geographic isolation, subtle habitat differences, and differences in phenology. Though the floral morphology of *D. hendrixii* and *D. attenuata* subsp. *attenuata* are similar enough that pollinators may visit both, the differences in habitats, dormancy, and vegetative morphology may prevent the establishment of frequent successful hybrids. There were no obvious

hybrids between *D. hendrixii* and other nearby *Dudleya* taxa observed in the wild.

Conservation and Threats

As of 2015, ongoing expansion of agricultural lands and urbanization potentially threaten the population. Additionally, the planned Port at Colonet could bring approximately 200,000 new people, transforming a barely populated stretch of Baja California to a port built to rival the Los Angeles/ Long Beach Port, at an initial cost of $4 billion or more (Dickerson 2008). At this time, however, the port proposal has been withdrawn. If the port project goes through in the future, the pressure for railroads, roads, housing, and the accompanying development for a new city would be expected to be intense. Berry farming is also currently expanding in the areas near this species, with elimination of significant areas of native habitat.

TAXONOMIC KEY

A revised key to species of subg. *Hasseanthus*, modified from Dodero and Simpson (2012) and McCabe (2012), is presented below.

1. St gen above soil surface, often elongate, often branched; lvs gen evergreen, ± not petioled, petals ascending to erect (remaining *Dudleya* species)
1′ St gen below soil surface, not elongate, gen simple, unbranched; leaves deciduous, vernal, generally petioled (barely in *D. crassifolia*), petals ascending to spreading (subg. *Hasseanthus*)
  2. Corolla consistently yellow; flower odor absent
    3. Leaves 4–15 cm long, linear, ± narrowed above base, tip sharply acute; petals basally connate 1–2 mm . . . . *D. multicaulis*
    3′ Leaves 1–7 cm long, oblanceolate to spoon-shaped, strongly narrowed above base (to gen 0.5–3 mm wide), tip acute to obtuse; petals basally connate 0.5–1 mm . . . . *D. variegata*
  2′ Corolla white to white-maroon (rarely pale yellow in *D. brevifolia* and *D. nesiotica*); flower odor musky-sweet or absent in *D. hendrixii*
    4. Leaf blade only slightly wider than petiole (ratio 1.2–1.4), petioles 2–3.3 mm thick; caudex with conspicuous, dried leaf bases persisting from multiple, previous seasons. . . . . *D. crassifolia*
    4′ Leaf blade two to more than four times as wide as the petiole (ratio 2.1–4.7), petiole 0.4–1.7 mm thick; caudex lacking conspicuous, dried leaf bases from previous seasons
      5. Petals ascending, 7–14 mm, 3.5–5.5 mm wide, fused 1–2 mm; fruit ascending; lf base 3–12 mm wide. . . . . *D. nesiotica*
      5′ Petals spreading, 5–10 mm, 2–4 mm wide, fused gen <1 mm; fruit spreading; lf base 1–4 mm wide
        6. Lower bracts <1.5x longer than wide; lvs 7–15 mm, ± spheric to spoon-shaped; petiole narrow. . . . . *D. brevifolia*
        6′ Lower bracts gen >2x longer than wide; lvs 10–60 mm, ± oblanceolate to club-shaped, to fusiform; petiole ± narrow
          7. Lvs 3–5, linear to fusiform, apex acute, not rounded. . . . . *D. hendrixii*
          7′ Lvs. usually >5, oblanceolate to club-shaped, apex rounded . . . . *D. blochmaniae*
            8. Lvs gen < 12, not to ± glaucous, 3–8 mm wide. . . . . subsp. *blochmaniae*
            8′ Lvs gen > 15, glaucous or ± so, 2–7 mm wide. . . . . subsp. *insularis*

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REVIEW
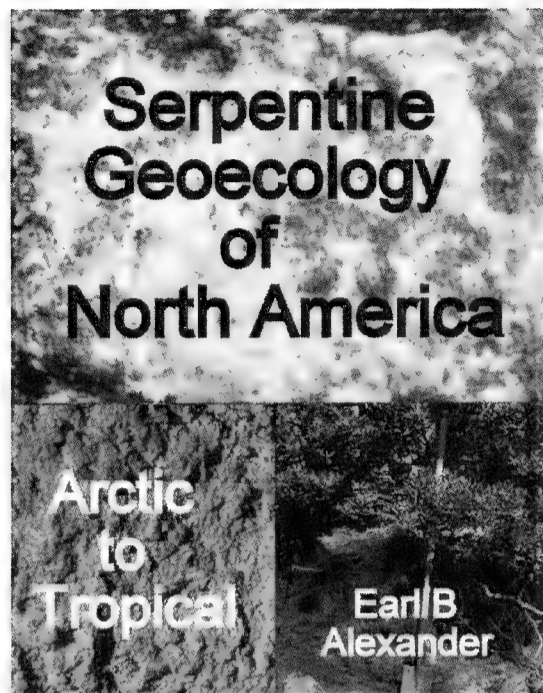
Serpentine Geoecology of North America—Arctic to Tropical, By EARL B. ALEXANDER. 2016. published by the author. [https://payhip.com/b/iEgY]. 209 pp. ISBN -978-0-9965548-1-7. Price $17.45 (PDF).

Earl Alexander is the leading authority on soils derived from ultramafic (serpentine) parent materials, having seen and studied more serpentine sites in North America than any other serpentine ecologist. Earl's ebook *Serpentine Geoecology of North America—Arctic to Tropical* (2016) is the expanded companion to his hardcover book *Serpentine Geoecology of Western North America* (Alexander et al. 2007).

The ebook expands on the hardcover book by including localities from Quebec and Newfoundland in eastern Canada; Appalachian Mountains of the eastern U.S., Montana and Texas in the central U.S., and countries of the Caribbean including Nicaragua, Costa Rica, Cuba, Guatemala, Hispaniola, and Puerto Rico.

The ebook is well-organized beginning by laying the foundation for serpentine geoecology with clear discussion and depiction of the origin of serpentine rocks; followed by how climate influences weathering of parent material and resulting physical and chemical composition of soils; and finally, how the combination of climate and soils influence the vegetation type supported at each site. Like the hardcover book, the ebook is heavy on soil taxonomy and physical and chemical properties, but still provides a good overview of biological communities for each locality. Vegetation descriptions for each locality are focused primarily on dominant species with occasional mention of serpentine endemic species at select localities.

The number of serpentine localities included in the hardcover book for the western U.S. is more extensive than the ebook. The ebook, however, is more detailed than the hardcover book in serpentine geology and soil formation descriptions and includes the additional sites in North America that the hardcover book does not. Together, the hardcover book and ebook provide a nearly comprehensive overview of serpentine localities of North America. Prior to Earl's studies, very little was known about the ecology of serpentine localities in sparsely populated or remote regions of North America including Alaska, western Canada, Montana, Texas, and Baja California. His descriptions of obscure and poorly studied serpentine localities are a major contribution to the field of serpentine geoecology of North America.

For consistency, I wish that the ebook followed a format more similar to the hardcover book with domain maps and locality numbering. I would have also preferred to see more consistency in how soil data is presented in the tables, particularly for exchangeable Ca and Mg and the molar ratio of the two, one of the most important soil chemical characteristics influencing the composition and productivity of serpentine vegetation. There are some glaring minor formatting and spelling errors in text and figures, but these do not detract significantly from the value of the wealth of information contained within.

Overall, Earl Alexander's ebook *Serpentine Geoecology of North America—Arctic to Tropical* is an invaluable expanded companion addition to *Serpentine Geoecology of Western North America* in providing a comprehensive overview of serpentine localities throughout North America and a must have for any serpentine ecologist.

—RYAN O'DELL, Natural Resource Specialist, Bureau of Land Management, Central Coast Field Office. rodell@blm.gov

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IN MEMORIAM

ARTHUR RICE KRUCKEBERG: GEOBOTANIST EXTRAORDINAIRE (1920–2016)

Art Kruckeberg passed away on May 25, 2016 at the distinguished age of 96. In his passing, the botanical community lost a passionate botanist, a skilled teacher, an avid gardener, and a dedicated conservationist. Art taught botany, biology, plant evolution, and a course in ornamental plants at the University of Washington, Seattle from 1950 to 1989 and served as the Chair of Botany there from 1971 to 1977. Art was author of numerous peer-reviewed publications in botany (30 publications counted on Web of Science; Thomas Reuters, New York, accessed July 6, 2016), many of which focused on the systematics, ecology, and evolution of serpentine plants, including three in *Madroño* in 1958 (14: 217–227), 1983 (30: 230–244), and 1995 (42: 458–469). He also wrote books on geobotany (1984, 2002, 2006), natural history (1991), and gardening (1982). Art was one of the founders and past presidents of the Washington Native Plant Society and a co-editor of its journal *Douglasia* for many years. Sarah Gage, who wrote an appreciation in celebration of Art's 80th birthday in 2000 (*Douglasia* 24 [3–4]: 5–10), remembers Art as "a grand old man of Washington botany, a mentor, and a mensch." Art was a giant in western North American botany, a dedicated teacher, a willing mentor, a rigorous scholar, and a devoted friend of native and ornamental plants. For much of his life, Art worked passionately and painstakingly to preserve natural habitat and to create a home for plants in his own backyard.

Art was dedicated to the field of serpentine ecology and was one of its most committed disciples since the mid-1940s. Art's pioneering efforts to use experimental approaches for understanding plant evolution on serpentine soils were fundamental to promoting serpentine plants as model systems for studies in evolutionary ecology. He was a teacher, a friend, and a mentor to many generations of serpentine ecologists from across the world. Art was a revered celebrity in the international serpentine ecology community, a close-knit family of over 150 researchers, including botanists, geologists, and soil scientists, from approximately 45 nations. Those of us who had the good fortune to botanize on serpentine outcrops with Art will always remember him for the infectious fascination with which he talked about serpentine plants, whether they were ones he had encountered often or those that were new finds. Art, the supreme "Dr. Serpentine," will be sorely missed by serpentine enthusiasts, his colleagues, and friends for years to come.

Art grew up in South Pasadena, CA, where he fell in love with plants at a young age. He pursued his passion for plants at Occidental College, where he received a B.A. in Botany in 1941. The summer after his graduation, Art began working as an assistant for the renowned evolutionary botanists Jens Clausen, David Keck, and William Hiesey at the Carnegie Institution of Washington's Depart-
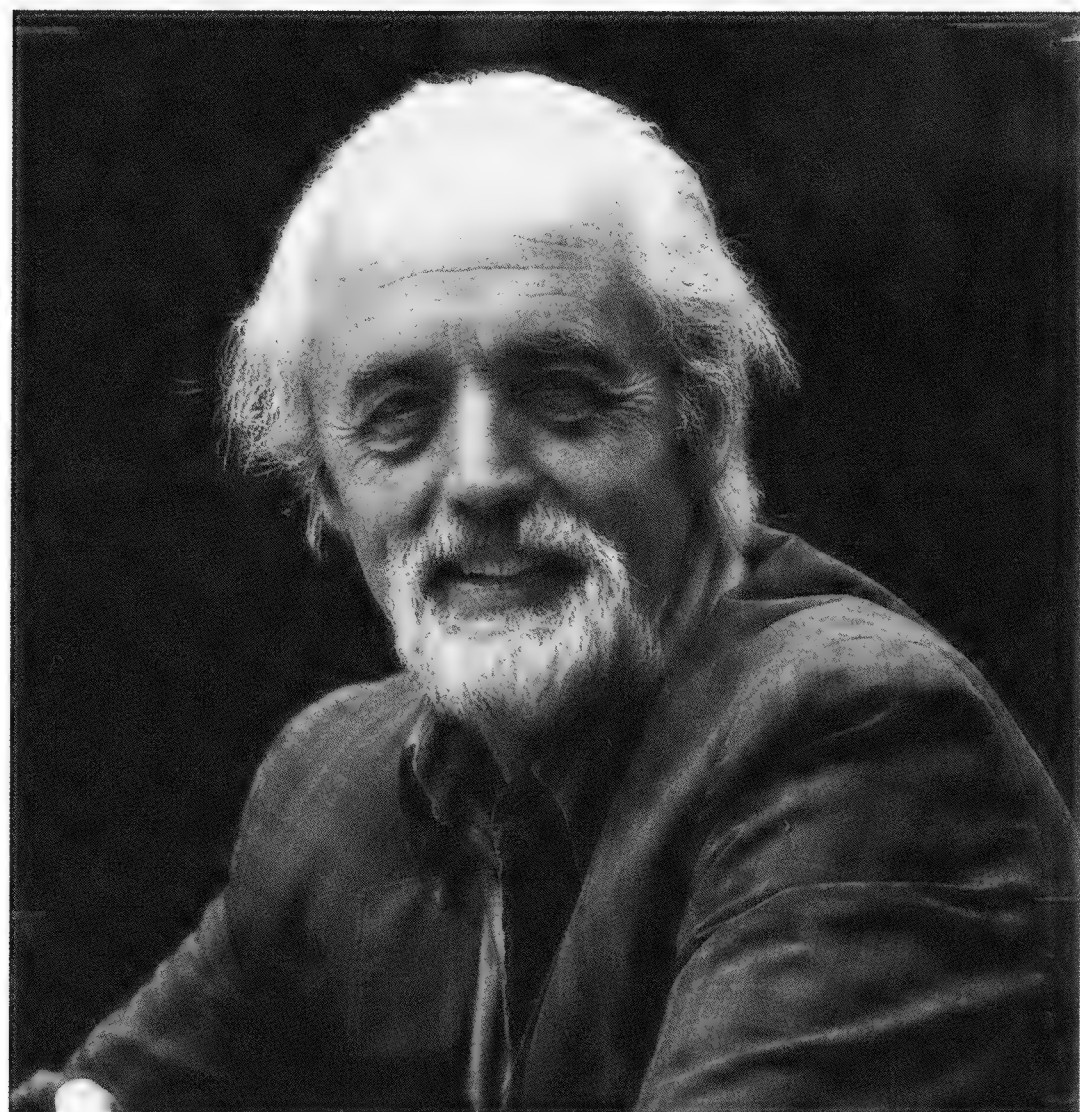
Art Kruckeberg as Chair, Department of Botany, University of Washington, Seattle. Courtesy Kruckeberg Botanic Garden Foundation

ment of Plant Biology at Stanford University (he began his graduate studies there shortly afterwards). However, his graduate tenure was cut short due to the Second World War, when he was enlisted as a Japanese language expert for the US Navy. While Clausen, Keck, and Hiesey went on to publish some of the most-cited works on experimental approaches to understanding the genetic structure of plant populations and adaptive evolution (see Núñez-Farfán and Schlichting 2001, *Quarterly Review of Biology* 76: 433–457), Art spent the war years translating Japanese documents. In 1946, Art entered the University of California, Berkeley where he earned a Ph.D. in Botany in 1950. Art's dissertation, "*An Experimental Inquiry into the Nature of Endemism on Serpentine Soils,*" had all the hallmarks of the early training he received from Clausen, Keck, and Hiesey; however, his focus on serpentine plants was clearly influenced by his graduate committee, consisting of Herbert Mason (phytogeographer), Hans Jenny (soil scientist), and G. Ledyard Stebbins, Jr. (evolutionary botanist and co-contributor to the modern synthesis). Mason had published two seminal papers on edaphic endemism in 1946 (*Madroño* 8: 209–216; 241–257) and encouraged Art to study the nature of plant endemism on serpentine soils. Art's first publication in 1951 (*American Journal of Botany* 38: 408–419), titled "*Intraspecific variability in the response of certain native plant species to serpentine soil,*" is one of the most influential papers on ecotypic differentiation in serpentine-

Author botanizing on a serpentine outcrop in Cuba with Art Kruckeberg during the mid-conference tour of the Fourth International Conference on Serpentine Ecology (2003). Photo Credit: Micheal Davis

tolerant plants, highlighting the use of common garden and reciprocal transplant approaches to understanding the evolutionary process. This paper, along with his 1954 paper titled *"The ecology of serpentine soils. III. Plant species in relation to serpentine soils"* (*Ecology* 35: 267–274), were critical in demonstrating the role of serpentine soils as selective agents in plant evolution. For a review of how Art's early research shaped the study of edaphic factors as stimuli for plant evolution, particularly the origin of serpentine-endemic taxa, see the article by Brian Anacker (2014, *American Journal of Botany* 101: 219–224).

While I did not have any formal associations with Art, my serpentine journey began with exposure to his writing early in my undergraduate years at College of the Atlantic (COA). In 1991, as a sophomore at COA, I took a course in plant systematics with the late botanist Craig Greene. During his lecture on plant endemism, Craig brought up serpentine-endemic plants of western North America, citing Art's work on ecotypic differentiation. At the end of the class, I wanted to know more about serpentine plants. Craig

gave me two photocopied papers (both of which I still proudly own): *"Soil diversity and the distribution of plants, with examples from western North America"* (1969, *Madroño* 20: 129–154) and *"An essay: The stimulus of unusual geologies for plant speciation"* (1986, *Systematic Botany* 11: 455–463). These eloquent papers implanted in me a deep desire to see serpentine plants of western North America and to think about the study of plant evolution under the serpentine influence as a fruitful area for graduate study. In Art's own words, "the serpentine bug had bitten me" even before I had seen a serpentine outcrop or a serpentine-endemic plant. This newfound fascination took me to the Department of Botany at the University of British Columbia, in 1995, where I pursued my M.Sc. under the supervision of Bruce Bohm. Soon after I published my first paper on edaphic differentiation in the *Lasthenia californica* (Asteraceae) complex (1999, *American Journal of Botany* 86: 1576–1596), I received a letter in the mail from none other than Art Kruckeberg. In his letter, Art congratulated me on a "fine-piece of work" and said, "more work should be done looking at how edaphic heterogeneity within serpentine outcrops contributes to plant distributions and ecotypic differentiation." This was my first personal interaction with Art, and getting his stamp of approval and nudge for additional work was the impetus I needed during a time when I was deciding whether to continue with a Ph.D. or return to my homeland, Sri Lanka. I was deeply touched by how someone of his stature could take the time to write to a novice and a stranger like myself, and replied immediately, thanking him profusely. A few months later, upon his invitation, I visited Art in his office at the University of Washington. Upon asking for directions to his office, I was told to "follow the smell of the tobacco and the sounds of the typewriter, Art will be behind those doors." I quickly realized how precise these odd directions were. Knocking on his door I heard "enter" in a deep and commanding voice. Meeting Art for the first time was truly a humbling experience. He looked quite the distinguished gentleman, spectacled and neatly dressed (with suspenders, of course), a lighted pipe in his hand, and an old typewriter at his desk; there was a freshly typed page still dangling on the side of the machine and Art still deep in thought. After saying hello, he asked how I came to be called "Nishi." When I explained to him that I had spent my early years in Japan, he smiled and said, "Aha, I knew that" (Nishi means west in Japanese). We talked about our shared experiences of a foreign land, decades apart. He then inquired about Sri Lanka and whether the civil war had made me flee the island; when I said yes, he wanted to know more. Twenty minutes into the meeting, we were still chatting about foreign lands, languages, ethnic conflicts, and food when he looked straight at me and said "would you like to be a teaching assistant for a geobotany course I am co-teaching with Robert 'Bob' Coleman [eminent Stanford geologist and fellow serpentine enthusiast]?" I was stunned but said yes. That summer I was off to the Siskiyou Field Institute in Cave Junction, OR, to assist in teaching a course about the geobotany of a place I knew nothing about! That was how Art came into my life; he sensed my drive to learn and my fascination with a system he, too, had fallen in love with and he did what he could to help me realize my dream. Art was

generous with his time and I learned much during my two weeks with him and Bob. In return, I was the designated driver for Art when he wanted to explore the nearby vineyards for the tasting of southern Oregon wine. This gave me the great pleasure of chatting away with Art about plants and soils and about his family and life while he enjoyed the many flavors of Oregon grapes. Art had a way with people; he was generous with his time and expertise, and he was always gracious in his interactions with those young and old, amateur and professional. He was always ready to give and encourage those who needed some words of wisdom or a letter of recommendation.

Susan Harrison, plant ecologist and fellow serpentinophile from the University of California, Davis, fondly remembered Art for his graciousness, sincerity, and optimism:

"In 2001, Art gave a seminar at Davis and we took a field trip to explore the serpentines at McLaughlin Reserve. He drew an incredible turnout: a full house of 100+ and 25 to 30 for the field trip. His talk was wonderful, full of the kinds of details that Art is legendary for (the names of plants he saw at specific locations on a field trip 40 years ago, etc.). Our community was really enchanted by the chance to see a living legend from the golden era of the modern synthesis. Art's tremendous graciousness manifested when I arrived late at the train station to find him peacefully sitting on a bench in a light rain, and also when the field trip turned out to be cold and wet and our hike a little rougher than expected. He just seemed to tolerate every little adversity with such a greatness of spirit, and was always ready to turn the conversation to a more pleasant topic. I also remember that when some of us were bantering in our slightly cynical everyday fashion, he didn't participate, and later made a mild comment about our 'fin-de-siècle' attitude. That stuck with me because it exemplified what a Greatest Generation member he was—so full of sincerity and optimism, so lacking in negativity and self-indulgence."

Robert Boyd, another plant ecologist and fellow serpentinophile from Auburn University, warmly recalled Art's energy and enthusiasm for all things geobotanical:

"In the early 2000s, I invited Art to come give a talk to my department [Biological Sciences]. Art was interested in going to the field while he was here, and my Ph.D. student at the time, Mincy Moffett (now a botanist for the Georgia Department of Natural Resources), and I took him to the famous Bibb Glades here in Alabama. These are places where the soils are derived from Ketona Dolomite, an unusually pure type of limestone. The rocky, open sites (surrounded by hardwood forest) host at least eight endemic plant taxa; the endemic plants and their community were only discovered in 1992! Given Art's abiding interest in geobotany, these were the perfect places to take him to show him unusual soils and endemic plants. With the able aid of Al Schotz, botanist for the Alabama Natural Heritage Program, we showed Art some of these interesting sites and some of the endemic plants. Art also expressed interest in seeing *Neviusia*

alabamensis (Rosaceae), which grows on limestone here in Alabama, because Art had a specimen in his garden of *N. cliftonii* collected from limestone in northern California (it is endemic to Shasta County and was discovered in the early 1990s). These are the only two species in the genus and they are disjunct by over 1,000 miles. Much to Art's delight, Al and Mincy managed to guide us to a spot where *N. alabamensis* was found, and Mincy later was able to obtain a living specimen, which he sent to Art. Years later Art reported that the specimen was alive and well in his garden, a memento of his visit to Alabama."

Alan Baker, co-founder of the International Conferences on Serpentine Ecology, and formerly of Sheffield and Melbourne universities, recalled the pleasure he always had talking to Art and seeing Art's great interest and enthusiasm in helping others:

"A real gentleman to be sure; one of the Titans of the geobotanical world. I vividly recall my first field visit to the Californian serpentines with Art and the late Joe Callizo of the California Native Plant Society as leaders on the mid-conference trip from UC Davis. His intimate knowledge of the very rich flora truly amazed me. Tony Bradshaw (my guru) also held Art in great esteem."

Roger Reeves, the other co-founder of the International Conferences on Serpentine Ecology, and formerly of Massey University, remembers Art's love for and relationship with serpentine:

"One of Art's long-held ambitions was to visit Dun Mountain near Nelson, New Zealand, one of the country's small number of ultramafic sites. The name was given by early settlers for its dun color, and when Austrian geologist Ferdinand von Hochstetter in 1859 discovered that its characteristic rocks were composed of olivine with small amounts of chromite, he named the rock dunite, and this became its type locality. As is often the case elsewhere, a well-defined vegetation change occurs at the sedimentary-ultramafic boundary, and several plant species are endemic to Dun Mountain. In November 1984, I accompanied Art to Dun Mountain. After a long walk through the forest we emerged suddenly onto the sparsely vegetated ultramafics. Art dropped to his knees and bowed his head in a sign of veneration to this historic site."

The International Conferences on Serpentine Ecology, held every 3–4 years since 1991, are venues where stories of Art are often reminisced and shared. The first conference was held at the University of California, Davis and was intended as a means of recognizing the life-long contributions to serpentine ecology by Art and two other leaders in the field, Robert Brooks and Ornella Vergnano Gambi. Presentations were made to each of the three honorees at the banquet dinner. The late Richard Walker, Art's long-time colleague at the University of Washington and fellow serpentinophile, commenting on Art's "way of living and working" in the conference proceedings, states:

"[Art] is gregarious, devoted to family and friends, an effective and sought after leader of field excursions and discussion groups, always ready to help others, and a wise

counsellor. He maintains an active correspondence with colleagues over the world, but in his own work and writing, he is an individualist, doing his plant trials by himself, making his own evaluations of results, formulating his own essays, and rarely collaborating with others. His greatest delights are in relaxation and reading (voracious and wide-ranging) and in growing plants.... We are all fortunate to have been influenced by this versatile serpentinophile."

Art attended three of the eight International Conferences on Serpentine Ecology: Davis, CA (1991), New Caledonia (1995), and Cuba (2003). I attended the conference in Cuba with Art and was thrilled to see him in action in the vast and diverse serpentine landscapes across the island. Art was fascinated with new plants he was encountering; I will always remember his almost child-like admiration of his "first encounters" and his willingness to learn from and share his knowledge with the locals. I also remember watching Art during conference presentations. Art would often doze off halfway through a talk but would wake up as soon as the presentation is over and raise his hand to ask one of the most probing questions of the talk. I, along with many other young researchers at the time, were always amazed at how he could ask such critical questions despite sleeping through much of the talk.

Art's other botanical- and conservation-oriented accomplishments included serving on the Editorial Board of *Madroño* and the advisory councils of the Washington Natural Heritage Program and the Center for Plant Conservation. During his long teaching career, he took great interest in undergraduate students and supervised numerous M.Sc. and Ph.D. students. Art and his wife, Mareen, shared a deep love for and admiration of plants, and together they shaped their four-acre property into a beautiful garden of native and ornamental plants. Their legacy will live on in the form of the Kruckeberg Botanic Garden and the MsK Rare and Native Plant Nursery, a public/private cooperation between the City of Shoreline and the Kruckeberg Botanic Garden Foundation. In recognition of Art's life-long efforts to promote botany, he was awarded the prestigious Peter Raven Award for public outreach in botany by the American Society of Plant Taxonomists in 2006.

In 2000, I had the great pleasure of writing in celebration of Art's 80th Birthday (see Botanical Electronic News Issues 244–246 for several articles by Art's former students and colleagues, including the late Richard Walker, Robert Coleman, and Rhoda Love; http://www.ou.edu/cas/botany-micro/ben/2000.shtml) and, now, I write with a deep sense of appreciation for having had the good fortune of knowing Art as a scholar, mentor, and friend. Art's life and work will be celebrated by the attendees of the 9th International Conference on Serpentine Ecology in Tirana, Albania, in June 2017.

Dr. Serpentine, you rock!

—NISHANTA RAJAKARUNA, Biological Sciences Department, California Polytechnic State University, CA; nrajakaruna@gmail.com

PRESIDENT'S REPORT FOR VOLUME 63

Dear Colleagues,

Another year has passed and the California Botanical Society has made some significant progress. As you probably already know, the Society started a new Student Research Grant in 2016, named in honor of Paul Silva who donated the initiating funds in his will. We presented one award in 2016, but the council plans to increase the number of awards in coming years. A notable feature of our new grant is the eligibility of undergraduate students in addition to graduate students. Look for a call for proposals soon. The Society will do everything within its means to increase support for student botanical research.

Speaking of students, the Annual Banquet of the Society and the biennial Graduate Student Meeting will take place in April 2017 at the Santa Barbara Botanic Garden. The exact date will be announced soon. Taking place every other year, the Graduate Student Meeting is one of the most important events sponsored by the Society. Remind students of this event now. We strongly encourage graduate students to submit an abstract and share their research projects with all of us. The previous meeting, which took place at Rancho Santa Ana Botanic Garden, was a great success and we anticipate that the upcoming meeting will be equally enjoyable. The annual banquet will follow the student meetings at the Garden. Last year's banquet in Bakersfield was a success even with the unusual rain, and Phil Rundel's talk was the special gift of the evening. We look forward to visiting with old friends and meeting new ones in Santa Barbara.

A few other updates. As in previous years, the Society is sponsoring the mixer for the Northern California Botanists symposium in Chico. This is a good way to meet up and socialize before our annual banquet. We look forward to seeing you there. Our newsletter, *Nemophila*, is thriving and stimulating interest in botany and botanists thanks to the continuing efforts of our past-president Tom Parker. We encourage you to submit interesting material for the newsletter. Finally, *Madroño* continues to be on time thanks to the efforts of our editor, Matt Ritter, and continues to be the best outlet for botanical research in Western North America.

Finally, even though *Madroño* is now available online through BioOne, societies are really about the membership and getting together to share ideas. Encourage botanists that you know to join the Society, especially students, and participate in the annual meetings.

Thank you for your continued support.
Mark Brunell, October 2016

EDITOR'S REPORT FOR VOLUME 63

I am pleased to report the publication of Volume 63 of *Madroño* by the California Botanical Society (CBS) in 2016.

The publication of *Madroño* remains on schedule with an average time between initial submission and publication of about 7 months. I believe that *Madroño* is still the best outlet for western botanists to publish their work in a timely fashion, while reaching an interested and relevant audience.

The efforts of numerous individuals are critical to the continued quality of the journal. Chief among these is our editorial assistant, Genevieve Walden. I am so thankful for all her diligent work and assistance. Thank you as well to the Noteworthy Collections editor, David Keil. Steve Timbrook has long provided the Volume Index and Table of Contents for the journal and I thank him for his efforts. I am also grateful to our reviewers who volunteer time to assess the quality of submitted work.

It is an honor to continue to be Editor of *Madroño* and interact with so many great contributors and reviewers. Botany is alive and well in Western North America! The evidence is in *Madroño*. Please continue to submit your work to the journal and have a great year.

Matt Ritter
San Luis Obispo
October 2016

REVIEWERS OF MADROÑO MANUSCRIPTS 2016

Vanessa Ashworth
Bruce Baldwin
G. Kai Blaisdell
Peter Bowler
William Buck
Chris Campbell
Phil Cannon
Ben Carter
Tom Chester
Mark Darrach
James Freund
C. Matt Guilliams
Richard Halse
Judy Harpel
Kristen Hasenstab-Lehman
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Judy Sutherland
Dean Taylor
Genevieve Walden
Rich Walker
Gary Wallace
Eddie Watkins
Dieter Wilken
Carol Wilson
Paul Wilson
Dana Adrian York

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Classified entries: Major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

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Subscriptions—Membership

The California Botanical Society has several annual membership categories: Regular $50, family $55, emeritus $35, student $30 and life $1,000. Members of the Society receive Madroño free, in print and online, and can opt not to receive Madroño in print. Institutional subscriptions to Madroño are $85 per year. Membership and institutional subscriptions are based on the volume year of Madroño, which follows the calendar year. Applications for membership/institutional subscriptions and renewals may be made online or by sending the membership form (also available online) to the Membership Chair. Requests for changes of address, and Madroño delivery inquiries should be sent to the Membership Chair. Orders for back issues of Madroño may also be made online at calbotsoc.org or by sending the order form (available on line) to the Corresponding Secretary. Price and mailing cost inquiries for back issues of Madroño should be sent to the Corresponding Secretary.

Information for Contributors

Submit manuscripts to http://www.edmgr.com/madrono/. If you are submitting a manuscript for the first time to the Madroño PeerTrack website, you must first register by clicking "register now" and following the instructions. Manuscripts by authors having outstanding page charges will not be sent for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish Resumen and an English Abstract.

For all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.), follow the format used in recent issues for the type of item submitted. Detailed information for contributors, including instructions for manuscript preparation, is available at the California Botanical Society website, www.calbotsoc.org; follow the link for Madroño.

All California Botanical Society members current in the volume year that their contributions are published are allowed five free pages per volume year. Additional pages will be charged at the rate of $40 per page. Joint authors may apply all or a portion of their respective five-page allotments to a jointly-published article. Partial pages will be charged as full. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing Madroño on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for color plates and other complex matter (including illustrations, charts, maps, photographs) will be charged at cost. Author's changes after typesetting @ $4.50 per line will be charged to authors. Page charges are important in maintaining Madroño as a viable publication, and timely payment of charges is appreciated.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

VOLUME 63 OF MADROÑO IS DEDICATED TO PROFESSOR MICHAEL G. SIMPSON